

THE EVOLUTION AND SYSTEMATICS OF ONAGRACEAE: LEAF ANATOMY¹

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ABSTRACT

Using a collection of liquid-preserved vegetative shoots representing all 17 genera of Onagraceae, I investigated the cross-sectional histology of mature leaves. The study focussed on a search for systematically useful and diagnostic features as well as on the determination of possible trends of specialization of leaf features. Exclusively dorsiventral-leaved species are found in *Ludwigia*, *Hauya*, *Fuchsia*, *Circaea*, and *Lopezia*. Leaves of these genera also have the most prominent midrib structure. The most generalized anatomy including the presence of extraxylary fibers and diverse calcium oxalate crystal structure is found in *Fuchsia*, *Ludwigia*, and *Hauya*. The other twelve genera, which belong to the tribes Epilobieae and Onagreae, show a variety of leaf specializations including xeromorphic isobilateral structure, small midribs with small midveins, the absence of extraxylary fibers, the absence of druses and styloid crystals, and a poorly differentiated mesophyll. On the basis of correlations with data from wood anatomy, pollen morphology, reproductive biology, and biogeography, I hypothesize that the Onagraceae leaves show a general reduction in leaf complexity. Leaf anatomy by itself is not diagnostic for those genera with reduced structure but it may be distinctive in the genera with more complex structure such as *Fuchsia*, *Ludwigia*, and *Hauya*.

The Onagraceae as defined by Raven (1979) comprise 674 species and 17 genera arranged in seven tribes. The family clearly belongs to the order Myrtales (Cronquist, 1968; Dahlgren, 1980; Takhtajan, 1969), but it is very distinct within the order. Onagraceae are distinguished by a distinctive four-nucleate embryo sac, the absence of alkaloids, the presence of abundant raphide crystals in vegetative tissue, and a paracrystalline-beaded pollen ectexine together with viscin threads on the pollen (Raven, 1979). Some genera have other features that are common in other Myrtalean families, including bicollateral vascular bundles, interxylary phloem, and in some cases stipules. The family may have originated in South America, where the two most primitive genera, *Ludwigia* and *Fuchsia*, center, especially in view of the clearly austral distribution of the order. The family, however, has a strong secondary center of development of the derived groups Onagreae and Epilobieae in western North America (Raven, 1979).

In addition to the fact that the leaf anatomy of the family has not been investigated thoroughly and systematically, this study was undertaken for three reasons. First, a large and comprehensive collection of liquid-preserved shoots with leaves was put at my disposal by Dr. Peter Raven. Secondly, taxonomic studies of the Onagraceae in recent years have produced a nearly complete inventory of species and a good taxonomic understanding of relationships within genera, and to some extent, between genera (review in Raven, 1979). This work has been of great value in providing accurate names for specimens being investigated anatomically, a formidable problem with most angiosperm families. The existing

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intrageneric classifications provide useful frameworks for comparing hypotheses of the evolution of leaf features. Thirdly, a number of other thorough investigations of chemistry, anatomy, and cytology of the Onagraceae have made it probably the best known flowering plant family. A sample of these include studies on wood anatomy by Carlquist (1975, 1977); on pollen by Skvarla, Raven, and Pragowski (1975, 1976) and Skvarla, Raven, Chissoe, and Sharp (1977); on flavonoids by Boufford, Raven, and Averett (1978) and Averett, Kerr, and Raven (1978). Floral anatomy has been studied by Eyde (1978, 1981, 1983) and Eyde and Morgan (1973); seeds by Seavey, Magill, and Raven (1977) and Raven, Sharp, and Keating (in prep.); reproductive biology by Raven (1979) and leaf architecture by Hickey (in prep.).

The existence of these and other previous studies is especially important. While wood anatomy, pollen morphology, and leaf architecture all have well established trends of specialization anchored in the fossil record (Dickison, 1975; Doyle & Hickey, 1976), the same cannot be said of leaf anatomy. The leaf is commonly regarded as being very variable anatomically although its variations can concur with generic, specific, or familial lines (Carlquist, 1961). Any hypothesized trends of specialization produced from this study, however, depend heavily on correlations with conclusions or data from these other studies. Among xeric-adapted species, trends of specialization are becoming better known in the light of recent comprehensive studies such as those by Pyykkö (1966) and Böcher (1979). An understanding of this type of adaptation is important in evaluating the features of leaves of some Onagraceae.

The most comprehensive comparative studies of Onagraceae leaf anatomy are those of Solereder (1908) who included 11 genera, and those of Metcalfe and Chalk (1950), who also included 11 genera but more species. Other studies that supply generally smaller quantities of data are those of Dee (1977) on *Gaura*, Carlquist and Raven (1966) on *Gongylocarpus*, Kidwal (1965) on *Fuchsia*, *Epilobium*, and *Ludwigia*, Logan and Holloway (1934) on *Fuchsia* and *Epilobium*, and Suckling (1913) on *Fuchsia*. Leaf anatomy of *Oenothera* is described by Roth (1960), Shields (1951), and Reinke (1876).

The principal questions defining the limits of this study are systematic. In general, the first consideration is whether the data from leaf anatomy correlate with the generic or tribal delimitations based upon traditional taxonomic studies. Previous literature and personal communications from other students of Onagraceae have suggested looking at a few specific problems. These include the proper tribal alignment and relationships of *Hauya*, the degree of evolutionary separation among the existing tribes, and the extent that certain features such as different types of calcium oxalate crystals define the family of tribes or genera. Special attention was paid to the tribe Onagreae, which in taxonomic schemes (Raven, 1964, 1979) seems to occupy a derived position in the family. Specifically, is the Onagreae, with its 11 genera, a natural group or a polyphyletic group of genera with certain common specialized features?

MATERIALS AND METHODS

Liquid-preserved specimens representing 125 species from all 17 genera of Onagraceae were available for study. Species examined are listed following each

generic description. Specimens were collected and fixed in the field or, when marked with an asterisk, were greenhouse-grown from field-collected seed. All specimens are vouchered at MO.

Specimens for sectioning were removed from the center of each lamina and selected to produce sections of midrib and margin areas. Paraffin embedment (Johansen, 1940) was followed by sectioning at 10 μm and staining with Safranin-O and Fast Green-FCF. All descriptions were prepared from observations of leaf cross sections made perpendicular to the midribs and margins with the adaxial surface oriented uppermost in description and figure orientation. Some longitudinal and paradermal sections were made to check the orientation and dimensions of such features as extraxylary fibers and raphides. No chemical determinations were made on crystal types or on materials here called "tannins" or "gummy sheaths." Punch cards and regression analyses were used in an attempt to discern clustering or other significant patterns of feature occurrence.

OBSERVATIONS

Boisduvalia (Figs. 23–24)—The lamina is dorsiventral tending toward isobilateral and is usually thin (120–160 μm). Epidermal layers are approximately equal in thickness, smooth, and with no apparent cuticle. Stomata are common on both surfaces. Single-celled trichomes are either smooth or striate-papillate. The mesophyll is usually poorly differentiated but has one or two rows of palisade cells. Midribs are small with no distortion of the adaxial surface and a slight rounding of the abaxial surface. The midvein is a short arc with a band of abaxial phloem extending adaxially and medially around the ends of the xylem arc but not connecting in the center. Ground tissue surrounds the midveins between the epidermal layers. Laterally, the mesophyll boundary is fairly sharp and is concave, convex, or irregular. Coarse raphides found in *B. subulata* are high, low, or in mid-mesophyll, arranged horizontally and parallel to the leaf axis. Fine raphides found in other species are in thick gum sheaths, mostly horizontal in mid-mesophyll. In *B. densiflora*, the gum sheaths are dense and sclereid-like with no raphides actually seen.

Specimens examined:

B. cleistogama Curran, *Crampton* 9222, California, cult. MO. *B. densiflora* (Lindley) S. Watson, *Seavey* 1095, California, cult. MO. *B. macrantha* Heller, *Seavey* 864, California, cult. MO. *B. subulata* (Ruiz & Pavón) Raimann, *Cheese & Watson* 4405 (K) Chile, cult. MO.

Calylophus (Figs. 38–40)—Leaves are isobilateral or dorsiventral (in one specimen) and variable in lamina thickness (95–400 μm). Epidermal layers are equally thick on both surfaces with no cuticle or apparent markings. Stomata are found on both surfaces except abaxial only in the dorsiventral specimen, *C. hartwegii*. The single-celled trichomes are finely tuberculate or striate-tuberculate. Very short rounded trichomes are uncommon in *C. berlandieri*. The mesophyll is usually well-differentiated with two layers of palisade cells beneath both surfaces. One layer of palisade is present in *C. hartwegii* where more than half of the mesophyll is spongy tissue. The midrib is small beneath the level adaxial surface and with only a small protrusion abaxially. The midvein is a short arc with a thin row of abaxial phloem and with a small patch of adaxial phloem seen in only one

specimen. The midvein is surrounded by ground tissue except in one specimen of *C. berlandieri*, in which ground tissue was reduced to small patches above and below the vein extending to the epidermis. In that specimen the palisade cells near the vein appeared to radiate from the vein curving toward either epidermis. In other isobilateral specimens the chlorenchyma boundary is concave, curving symmetrically around the midvein ground tissue. In *C. hartwegii*, the chlorenchyma is irregularly bounded by the midvein ground tissue. The leaf margin is rounded and normal except for the presence of a collenchymatous ridge in *C. berlandieri*. Fine raphides are common, horizontally oriented in mid-mesophyll, and unsheathed. In one specimen of *C. berlandieri*, the raphides are vertical in the palisade layers in heavy gum sheaths. In the same specimen, some are thin-sheathed and horizontal in mid-mesophyll.

Specimens examined:

C. berlandieri Spach subsp. *berlandieri*, Raven 26555, Kansas; Rowell 16089, Texas. *C. hartwegii* (Benth.) Raven subsp. *pubescens* (A. Gray) Towner & Raven, Powell & Powell 2827, Texas. *C. toumeyii* (Small) Towner, Towner 107, Arizona.

Camissonia (Figs. 30–32, 50–51)—The leaves are dorsiventral or isobilateral with the lamina ranging from 110 to 340 μm in thickness. Epidermal layers may be equally thick or somewhat thicker adaxially. No cuticle is distinguishable. Stomata are common on both surfaces. Trichomes are common to uncommon. Most are tuberculate, some are smooth or striate-ridged. The mesophyll is usually weakly differentiated with a palisade consisting of two cell layers or sometimes one. When spongy cells are present, the palisade occupies about half of the mesophyll. The midrib ranges from totally immersed in *C. sceptrostigma* and *C. andina* to having pronounced abaxial and adaxial ridges in *C. ovata*. The midvein is a small arc or occasionally a broad arc with a band of abaxial phloem. About half of the specimens show small patches of adaxial phloem near the margins of the xylem. Commonly, the midrib ground tissue extends between both epidermal layers with the mesophyll forming a convex boundary into the midrib. In *C. sceptrostigma* and *C. claviformis*, the palisade layer is continuous over the reduced midvein. Coarse or fine raphides may be present anywhere in the mesophyll including vertically in the palisade layer. Raphides, 40–60 μm long, are found in gum sheaths that may vary from 44 μm when resembling palisade cells to up to 300 μm long as horizontal sheaths.

Specimens examined:

C. andina (Nutt.) Raven, R. Olds, s.n., 12 Jul 1976, Oregon. *C. bistorta* (Nutt. ex Torrey & A. Gray) Raven, Knight s.n., s.d., California, cult., LA. *C. cheiranthifolia* (Hornem. ex Sprengel) Raven subsp. *cheiranthifolia*, cult. LA. *C. claviformis* (Torrey & Frémont) Raven, Thompson 3816, California. *C. lewisii* Raven, Thompson 3747, California. *C. ovata* (Nutt. ex Torrey & A. Gray) Raven, Thomas s.n., 20 Feb 1977, California. *C. pallida* (Abrams) Raven subsp. *hallii* (Davids.) Raven, Thomas 18473, California. *C. sceptrostigma* (Brandege) Raven, Nobs 8236, Baja California, Mexico, cult. DS, MO.

Circaea (Figs. 12–16)—The dorsiventral lamina varies in thickness from 90 to 250 μm . The adaxial epidermis is often two times as thick as the abaxial and there is apparently no cuticle. Stomata are abaxial only except in *C. cordata* where they are common on both surfaces. Trichomes are tuberculate or striate-

tuberculate. The mesophyll is usually differentiated with the one-layered palisade zone occupying one third of the mesophyll. The midrib varies from being prominent abaxially in *C. lutetiana* to totally immersed in *C. cordata*. Adaxially, the midrib may be slightly convex. Midvein xylem varies from a broad arc in *C. lutetiana* to a very small arc in *C. cordata*. Phloem forms a band abaxial to the midvein xylem in all specimens and, in the larger veins, forms two adaxial bands extending from the ends of the xylem arc that do not contact medially. The midvein is surrounded by ground tissue that is irregularly demarcated from chlorenchyma of the adjacent lamina. In *C. cordata*, the palisade layer is confluent adaxially over the midvein. Fine raphides are present, sheathed or unsheathed, mostly horizontal in mid-mesophyll.

Specimens examined:

C. alpina L. subsp. *pacifica* (Aschers. & Magnus) Raven, *Kruckeberg s.n.*, 1976, Washington. *C. cordata* Royle, *Raven s.n.*, Jul 1975, Main Botanic Garden, Moscow (seed from Vladivostok region), U.S.S.R., cult. MO. *C. erubescens* Franchet & Savat., *Sohma s.n.*, Sep 1975, Japan. *C. lutetiana* L. subsp. *quadrisulcata* (Maxim.) Aschers. & Magnus, *Raven s.n.*, Jul 1975, Main Botanic Garden, Moscow (seed from Vladivostok region), U.S.S.R., cult. MO.

Clarkia (Figs. 41–42)—Leaves are dorsiventral except isobilateral in *C. rubicunda* and *C. purpurea*. The lamina varies from 190 to 310 μm in thickness. In all dorsiventral leaves, the adaxial epidermis is always thicker than the abaxial. No cuticle is discernable. Stomata are common on both surfaces in almost all specimens. Trichomes are absent in several specimens. Where present, the trichomes are often very broad and short but sharp tipped and slightly recurved. Some trichomes are straight, long, and thin-walled. All trichomes show fine, striate-papillate or tuberculate surfaces. The mesophyll varies from well to poorly differentiated and palisade layers may be one or two cell layers thick. The midribs are generally small with slight abaxial ridges except in *C. unguiculata*, which has a prominent abaxial ridge. The mid-veins are normally a narrow arc with an abaxial band of phloem adjacent to the xylem. Only in *C. rubicunda* is any adaxial phloem seen immediately adjacent to the xylem margins. Ground tissue around the midvein is not extensive and the boundary with chlorenchyma is variable and often irregular. Fine raphides are mostly present and are found in ovate-shaped gum sheaths oriented horizontally in mid-mesophyll. In *C. rubicunda* some raphides are vertical in the palisade layer. In *C. concinna*, discrete pairs of raphide clusters often share the same gum sheath.

Specimens examined:

C. breweri (A. Gray) Greene, *Roderick 09*, California. *C. concinna* (Fischer & C. Meyer) Greene, *Roberts s.n.*, Aug 1953, California, cult. LA. *C. cylindrica* (Jepson) Lewis & Lewis, *Lewis 1433*, California, cult. LA. *C. exilis* Lewis & Vasek, *Lewis 1429*, California, cult. LA. *C. purpurea* (Curt.) Nelson & J. F. Macbr. subsp. *quadrivulnera* (Douglas) Lewis & Lewis, *MacSwain s.n.*, s.d., California, cult. UC. *C. rubicunda* (Lindley) Lewis & Lewis, s. col., California, cult. RSA. *C. unguiculata* Lindley, *Lewis 1430*, California, cult. LA.

Epilobium (except sect. *Chamaenerion*; Figs. 17, 18, 20, 22, 49)—Leaves are dorsiventral or isobilateral in most sections. *Epilobium minutum* (sect. *Crosso-stigma*), a spring annual, is dorsiventral. Lamina thickness ranges from 90 μm to 260 μm . Epidermal layers are approximately equally thick or either layer may be

somewhat thicker. In sect. *Cordylophorum*, the cuticle or epidermal wall is striate all over. This is also seen in *E. canum* (sect. *Zauschneria*) and in *E. oreganum* (sect. *Epilobium*). Otherwise the cuticle is not seen and the surface is smooth or sometimes striate at the margins. Stomata are common on both surfaces. Trichomes are quite variable in length and sculpturing. They may be smooth, faintly or heavily striate, tuberculate or finely papillate. The mesophyll is usually poorly differentiated with a one- or two-layered palisade. Midribs may be prominent abaxially and sometimes adaxially but more commonly are grooved or level adaxially. Midribs may be completely immersed in *E. suffruticosum*. While some midveins may be broad arcs, they are more commonly reduced to small arcs. Abaxial phloem is present adjacent to the xylem but adaxial phloem is present only in the larger midribs. Adaxial phloem is never more than small patches adjacent to the ends of the xylem arc. Tannins are very uncommon but form dense deposits in the epidermal layers of *E. consimile* and in a few cells around secondary veins of *E. hornemannii* subsp. *behringianum*. Coarse raphides are found in *E. canum*, either sheathed or unsheathed and oriented parallel to the midrib in the upper and lower mesophyll. All other species have fine raphides in gum sheaths, often horizontal in mid-mesophyll but often found in any orientation. Very long sheaths may be found in *E. coloratum*.

Specimens examined:

E. canum (Greene) Raven subsp. *canum*, Seavey s.n., 1975, California, cult. MO. *E. canum* (Greene) Raven subsp. *latifolium* (Hook.) Raven, Seavey 809, California. *E. ciliatum* Raf. subsp. *ciliatum*, Raven 26540, Colorado. *E. coloratum* Biehler, Quebec, cult. MTJB 7499, cult. MO, Raven 26289. *E. consimile* Hausskn., Dolgachera s.n., 1975, Crimea, U.S.S.R., cult. MO. *E. glabellum* Forster f., New Zealand (CHR 191388). *E. glaberrimum* Barbey subsp. *fastigiatum* (Nutt.) Hoch & Raven, Hoch 1103, Washington, cult. MO. *E. hornemannii* Reichenb. subsp. *behringianum* (Hausskn.) Hoch & Raven, Dick 290, Alaska, cult. MO. *E. komarovianum* H. Lév., New Zealand (CHR 191393). *E. leptophyllum* Raf., Raven 26564, Wisconsin; Olson s.n., 1974, Newfoundland, cult. MO. *E. melanocaulon* Hook., New Zealand (CHR 191392). *E. minutum* Lindley ex Lehm., Howell 51156, California, cult. MO. *E. nevadense* Munz, Seavey 808, Nevada, cult. MO. *E. niveum* Brandegees, Bowman 1192G, California. *E. oreganum* Greene, Seavey s.n., 1975, Oregon. *E. oregonense* Hausskn., Hoch 755, Oregon, cult. MO; Hoch 823, Oregon, cult. MO. *E. palustre* L., Boufford 18795, Ontario. *E. paniculatum* Nutt. ex Torrey & A. Gray, Seavey s.n., 1975, Oregon, cult. MO. *E. pyrricolophum* Franchet & Savat., Kubota s.n., 1974, Japan, cult. MO. *E. suffruticosum* Nutt., Raven 26464, Wyoming.

Epilobium sect. *Chamaenerion* (Figs. 19, 21)—Leaves are dorsiventral except isobilateral in *E. dodonaei* and *E. fleisheri*. The lamina ranges from 110 μ m thick in *E. angustifolium* to 330 μ m in *E. fleisheri*. Epidermal layers are equally thick. Cuticle or epidermal walls may be smooth or finely striate throughout. Stomata are common on both surfaces. Trichomes have narrow bases, may be nearly smooth-walled or more obviously erose-striate ridged. The mesophyll is poorly differentiated with the palisade being single-layered in dorsiventral leaves and two-layered beneath both surfaces in isobilateral specimens. The midrib is prominent abaxially and has a smaller adaxial ridge in *E. angustifolium*. In the other specimens, the midrib is largely immersed. The midvein is a broad or narrow arc of xylem with an abaxial band of phloem. Adaxial phloem is formed in two large bands extending medially from the ends of the xylem in *E. angustifolium* and *E. latifolium*. Adaxial phloem is reduced or absent in other specimens. Midrib ground tissue ranges from abundant in *E. angustifolium* to nearly absent in *E. fleisheri*.

The mesophyll boundary is irregular and often indistinct. Tannins or other granular contents are occasionally present in enlarged cells of the mid-mesophyll. Fine raphides are present, thin-sheathed or unsheathed, vertical in the palisade layer or horizontal anywhere in the mesophyll.

Specimens examined:

E. angustifolium L. subsp. *circumvagum* Mosquin, *Raven* 26532, Colorado; *Boufford* 18747, Ontario. *E. dodonaei* Villars, *Davis & Polunin* 550019, cult., Royal Botanic Garden, Edinburgh. *E. fleischeri* Hochst., s. col., France (seed from Alps), cult. MO. *E. latifolium* L. subsp. *latifolium*, *Raven* 26533, Colorado; *Hoch* 1403, Alberta.

Fuchsia (Figs. 1–3)—The lamina is dorsiventral and thin (120–180 μm). The adaxial epidermis is slightly thicker or up to twice as thick as the abaxial epidermis. No cuticle is apparent. Stomata are found exclusively on the abaxial epidermis. Trichomes are smooth-walled in most specimens but finer or coarser tuberculate surfaces are present in *F. boliviana* or *F. parviflora*. The mesophyll is well- or weakly differentiated and the palisade always consists of a single layer that occupies about one-third of the mesophyll. The midrib is very large abaxially in *F. boliviana*, *F. ravenii*, *F. lycioides*, and *F. arborescens* but smaller in other species. The midrib is totally immersed in *F. thymifolia* and *F. procumbens*. In species with larger midribs, the adaxial side also forms a small ridge. The midveins range from a well-formed semicircle in *F. boliviana* to broad arcs in most other species to a very small vein in *F. thymifolia*. Phloem forms a band abaxial to and adjacent to the xylem. In species with larger midribs the phloem also forms patches adaxial to the xylem and adjacent to it. In *F. ravenii* and *F. arborescens*, the phloem forms several series of patches within the midrib area. Species with large midribs have ground tissue surrounding the vein and extending to both epidermal layers. The ground tissue mesophyll boundary is variable and irregular. In *F. ravenii*, the mesophyll is continuous across the midrib and above the vein. Raphide crystals are occasionally coarse, mostly fine, and sheathed or unsheathed. The sheaths often appear paired. The raphides are oriented horizontally in mid-mesophyll or may be vertical in the palisade layer. Some specimens show oblique or completely random raphide orientation.

Specimens examined:

F. arborescens Sims, *Breedlove* 15832, Guerrero, Mexico, cult. UC. *F. boliviana* Carrière, cult. LA, *H. Lewis* s.n., cult. MO. *F. encliandra* Steudel subsp. *encliandra*, *Breedlove* 7178, Oaxaca, Mexico, cult. UC. *F. lycioides* Andrews, *H. Mooney* s.n., 1972, Chile, cult. MO. *F. microphylla* Humboldt, Bonpland & Kunth subsp. *quercetorum* Breedlove, *Breedlove* 5972, Chiapas, Mexico, cult. UC. *F. parviflora* Lindley, *Breedlove & Gregory* 14251, Durango, Mexico, cult. UC. *F. procumbens* R. Cunn., New Zealand, Tasman Botanical Garden, cult. UC. *F. ravenii* Breedlove, *Breedlove* 15860, Oaxaca, Mexico, cult. UC. *F. thymifolia* Humboldt, Bonpland & Kunth subsp. *thymifolia*, *Breedlove* 15865, Oaxaca, Mexico, cult. UC.

Gaura (Figs. 33–37)—Two-thirds of the specimens have isobilateral leaves with the remainder being dorsiventral. Thickness ranges from 130 to 290 μm . Epidermal layers are equal on isobilateral leaves and thicker adaxially on dorsiventral ones. A cuticle is generally not apparent except at the leaf margins or abaxial midribs, where it may be striate-ridged. Stomata are common on both surfaces. Trichomes are thin or thick-walled, smooth or finely papillate or strongly tuberculate. The mesophyll is well-differentiated or poorly differentiated and the

palisade tissue is always 2–3 layered. The midrib is usually prominent forming equal-sized rounded ridges on both surfaces in most isobilateral specimens. The midvein is a broad arc or a small arc in *G. biennis*. The phloem forms an abaxial band adjacent to the xylem. In all specimens except *G. biennis*, the phloem also forms a pair of adaxial bands extending medially from the ends of the xylem arc and which may or may not be directly adjacent to the xylem. The midrib ground tissue extends from the vein to both epidermal layers. In the larger isobilateral leaves with large midribs, mesophyll tissue extends into the midrib zone forming a symmetrical concave boundary against the midrib ground tissue. Leaves with smaller midribs show a less regular mesophyll boundary. Most leaves have fine raphides but coarse raphides occur in *G. suffulta* and *G. angustifolia*. Raphides may be with or without gum sheaths. They are horizontal in mid-mesophyll or often vertical in the adaxial or abaxial palisade. The heavy gum sheaths may resemble sclereids in *G. lindheimeri*, *G. demareei*, and *G. longiflora*. Druses were seen in a specimen of *G. angustifolia*. *Gaura longiflora*, *G. demareei*, and *G. biennis* are very closely similar species of sect. *Gaura*, *G. angustifolia* and *G. lindheimeri* are less closely similar species of the same section.

Specimens examined:

G. angustifolia Michaux, Boufford 18409, Florida. *G. biennis* L., Sorensen 5111, Iowa, cult. MO. *G. demareei* Raven & Gregory, Hoff s.n., 1976, Texas. *G. lindheimeri* Engelm. & A. Gray, s. col., Texas, cult. UC. *G. longiflora* Spach, Boufford & Lorence 18864, Missouri. *G. mutabilis* Cav., Rzedowski 29135, Mexico, cult. MO. *G. parviflora* Douglas, Hoff s.n., 1976, Texas. *G. suffulta* Engelm. ex A. Gray subsp. *suffulta*, Benbow 75, Texas. *G. villosa* Torrey subsp. *villosa*, Raven 26552, Kansas.

Gayophytum (Fig. 29)—The leaves are isobilateral but have better developed palisade tissue on the adaxial side. The lamina is ca. 210 μm thick. Epidermal layers are of equal thickness and have no apparent cuticle. Stomata are common on both surfaces. Trichomes were not seen. The mesophyll is not well differentiated but there is a two layered adaxial palisade and one abaxial palisade. The midrib is slightly convex abaxially and slightly grooved adaxially. The midvein is a broad arc with an abaxial band of phloem adjacent to the xylem and two well-developed bands of phloem adaxially. They extend medially from the ends of the xylem but do not connect and are separated from the xylem by ground tissue. Ground tissue extends to the epidermal layers above and below the midvein but laterally the midvein ends are within the mesophyll. Fine raphides (to 60 μm long) in their gum sheaths are vertical in the adaxial palisade or horizontal in mid-mesophyll. Some laticifer-like long gum sheaths may extend to 250 μm .

Specimen examined:

G. heterozygum Lewis & Szweyk., Chambers 4227, Oregon.

Gongylocarpus (Figs. 25, 26)—The dorsiventral lamina varies in thickness from 130 to 250 μm . The adaxial epidermis is slightly thicker or up to double the thickness of the abaxial epidermis. Epidermal surfaces are smooth or slightly striate. Trichomes are absent or uncommon adaxially over the midrib. The single-celled trichomes have a thin, minutely tuberculate wall. Stomata have guard cell pairs of equal length and width (ca. 24–28 μm) and are common on both surfaces.

The adaxial surface is level over the midrib while the abaxial surface has a slight rounded protrusion. Midrib vasculature is a small flattened arc with 4–5 patches of abaxial phloem. Midvein ground tissue surrounds the vein and is demarcated from chlorenchyma by an irregular vertical boundary. In a smaller leaf the midvein is embedded in chlorenchyma except for a small abaxial patch of ground tissue. The well-differentiated chlorenchyma has a palisade layer slightly thinner than the spongy layer. Columnar palisade cells are well-formed or somewhat irregular. One layer of angular collenchyma may be present beneath both midrib epidermal layers. Raphide crystals, mostly in gum sheaths, are common and are either coarse or fine. Some bundles of prismatic crystals ($8 \times 40 \mu\text{m}$) may also be present. Crystal sheaths are up to $60 \mu\text{m}$ long and are horizontally oriented in mid-mesophyll.

Specimen examined:

G. rubricaulis Schlecht. & Cham., *Breedlove 41880*, Chiapas, Mexico, cult. MO.

Hauya (Figs. 7, 8)—The dorsiventral lamina is about $130 \mu\text{m}$ thick and the adaxial epidermis is slightly thicker than the abaxial. Epidermal layers are smooth but cuticle ridges are visible in the boundary depressions between epidermal cells. Stomata are restricted to the abaxial epidermis with guard cell pairs about $20 \mu\text{m}$ long and $16 \mu\text{m}$ wide. Trichomes have birefringent walls and are common on adaxial and abaxial surfaces of veins. They are often coarsely tuberculate. The mesophyll is well differentiated consisting of one palisade layer occupying one-third of the mesophyll. The midrib is very prominent abaxially with only a slight ridge adaxially. The midvein is a large, well developed, semicircle open adaxially. A prominent band of abaxial phloem is present and numerous adaxial patches of phloem are found in the ground tissue within the xylem semicircle. Outside of the abaxial phloem is a layer of extraxylary fibers. The secondary veins have adaxial fiber extensions. The midrib ground tissue is well-demarcated from the mesophyll with an irregularly shaped boundary. Tannins are present in the phloem region of the midrib and in about six abaxial layers of midrib ground tissue. Styloid crystals with pointed or blunt ends are common and variously oriented in mid-mesophyll and around veins. Druses are less commonly found and loosely clustered. They also occur around veins. Fine raphides in long gum sheaths (to $65 \mu\text{m}$) may also be common near veins.

Specimens examined:

H. elegans DC. subsp. *cornuta* (Hemsl.) Raven & Breedlove, *Raven and Breedlove s.n.*, s.d., Chiapas, Mexico, cult. UC. *H. heydeana* Donn. Sm., *Breedlove 42080*, Chiapas, Mexico, cult. MO.

Heterogaura (Fig. 43)—Leaves are dorsiventral with a lamina thickness of $160 \mu\text{m}$. The epidermal layers are equal in thickness and have no apparent cuticle. Stomata are common on both surfaces. Trichomes have thin, smooth walls and are uncommon. The mesophyll is not well-differentiated with the single palisade layer occupying about 40% of the mesophyll. The midrib is slightly ridged abaxially and has a small adaxial groove. The midvein is a small arc of xylem with a band of abaxial phloem. Small patches of adaxial phloem occur near the margins of the xylem. The midrib is surrounded by a small zone of ground tissue that

extends to the abaxial epidermis. It may extend to the adaxial epidermis or the palisade cells may be continuous over the vein. Commonly, the chlorenchyma is concave in its boundary with the ground tissue. Fine raphides in gum sheaths may be vertically oriented in the palisade tissue or may be horizontal in mid-mesophyll.

Specimen examined:

H. heterandra (Torrey) Cov., *Lewis 1628*, California.

Lopezia (Figs. 9–11, 48)—The leaves are dorsiventral with the lamina thin to thick (120–370 μm). Epidermal layers are mostly equal in thickness or slightly thicker adaxially. Adaxial epidermal cells may be uniformly or occasionally markedly convex in some species. No cuticle is apparent. Stomata are mostly abaxial only although a few specimens had adaxial stomata. Trichomes are absent or not seen in most specimens. The adaxial epidermal cells are papillate in *L. miniata*. When present, trichomes are sclerotic and smooth-walled. The mesophyll is usually well-differentiated and the one-layered palisade occupies approximately 30–50% of the mesophyll. The midrib usually is large, forming a prominent ridge abaxially while the adaxial surface is nearly level. The midvein is a large semi-circle in *L. grandiflora* and *L. langmaniae*, a broad arc in most other species or a small arc in *L. nuevo-leonis*. Phloem forms an abaxial band adjacent to the xylem, and in the larger midveins, some adaxial phloem is usually formed as individual patches or rows, not necessarily adjacent to the xylem. Midrib ground tissue surrounds the vein between the epidermal layers in the large midribs. The boundary with adjacent mesophyll is variable and irregular. In *L. ovata*, *L. gentryi*, and *L. nuevo-leonis*, the palisade is continuous adaxially to the midvein. In *L. langmaniae*, the adaxial phloem contains gum ducts oriented parallel to the vein. Fine raphides are present in all specimens and quite variable. They may be with or without gum sheaths and they may be horizontal in mid-mesophyll or vertical in the palisade layer. The raphides may be replaced entirely leaving “sheaths” resembling sclereids (*L. racemosa*, *L. miniata*, *L. nuevo-leonis*, *L. grandiflora*). Some sheaths are elongate resembling ducts.

Specimens examined:

L. concinna Raven, *Reveal and Hardy 4064*, Sinaloa, Mexico, cult. MO. *L. gentryi* (Munz) Plitmann, Raven & Breedlove, *Breedlove 15551*, Durango, Mexico, cult. MO. *L. grandiflora* Zucc. subsp. *grandiflora*, *Breedlove 39154*, Oaxaca, Mexico, cult. MO. *L. grandiflora* Zucc. subsp. *macrophylla* (Benth.) Plitmann, Raven & Breedlove, *Breedlove 22704*, Chiapas, Mexico. *L. langmaniae* Miranda, *Breedlove 7161*, Chiapas, Mexico, cult. MO. *L. longiflora* Decaisne, *Breedlove 8044*, Morelos, Mexico, cult. MO. *L. miniata* Lag. ex DC. subsp. *miniata*, *Boutin & Brandt 2165*, Jalisco, Mexico; *Carlquist s.n.*, Mexico, cult. Stanford, *Raven 66-22*. *L. nuevo-leonis* Plitmann, Raven & Breedlove, *Ripley & Barneby 13569*, Nuevo León, Mexico, cult. MO. *L. ovata* (Plitmann, Raven & Breedlove) Plitmann, Raven & Breedlove, *Breedlove 4255*, Durango, Mexico, cult. Stanford. *L. racemosa* Cav. subsp. *racemosa*, *Thompson 3797*, Mexico, cult. LA. *L. racemosa* Cav. subsp. *moelchenensis* Plitmann, Raven & Breedlove, *Breedlove 7794*, Chiapas, Mexico, cult. Jerusalem, *Plitmann 68-2*. *L. riesenbachia* Plitmann, Raven & Breedlove, *Anderson & Anderson 5626*, Oaxaca, Mexico, cult. MO. *L. semeiandra* Plitmann, Raven & Breedlove, *Breedlove 19163*, Sinaloa, Mexico, cult. MO. *L. suffrutescens* Munz, *Breedlove 24534*, Durango, Mexico, cult. MO.

Ludwigia (Figs. 4–6)—The leaves are always dorsiventral with the lamina thickness ranging from 60 to 190 μm . Thickness of epidermal layers is equal on

both surfaces. No cuticle is evident and epidermal surfaces are usually smooth. Striate ridges may be present abaxially on veins and at the margins in *L. peruviana* and *L. suffruticosa*. Stomata are equally common on both surfaces. Trichomes may be absent but when present are commonly single-celled. Walls are usually thin and smooth but they may be finely papillate or striate-papillate. Trichomes of *L. peruviana* are often 2-celled or up to 5–6 cells, unbranched. The mesophyll is well-differentiated with one adaxial layer of palisade occupying about half of the mesophyll. The midrib of the more generalized species is very prominent and rounded abaxially. There is also a high, flattened, adaxial ridge above the midrib. The midveins in these species are well-formed semicircles with an abaxial layer of phloem. Adaxially, the phloem forms small patches randomly in the ground tissue within the xylem semicircle. Species with this type of midrib-midvein anatomy include *L. erecta*, *L. lagunae*, *L. leptocarpa*, *L. maritima*, *L. peploides*, *L. peruviana*, *L. pilosa*, *L. polycarpa*, and *L. suffruticosa*. Other specimens studied show little or no adaxial ridge, less prominent rounding abaxially, a midvein consisting of a broad or smaller arc, loss of the adaxial phloem, and, in the smallest leaves, a continuous palisade layer across the adaxial side of the midrib. This more specialized type of leaf structure is found exclusively in some of the more advanced sections, such as sect. *Dantia*, but is scattered through the other groups as well. Patches of perivascular fibers are found abaxial to the midvein in *L. peruviana* and *L. suffruticosa*. The midrib ground tissue usually surrounds the midvein, and the boundary with the adjacent mesophyll is variously shaped. In the largest veins (*L. peruviana*) the palisade tissue curves upward into the adaxial ridge. Thick-walled secretory idioblasts are present just beneath both epidermal layers in *L. sedoides*, a floating aquatic plant. Calcium oxalate crystals are present in all samples of *Ludwigia*. Fine raphides are present in nearly all specimens and coarse raphides in five. Raphides are unsheathed and usually horizontal in mid-mesophyll. Druses are also present in a majority of specimens and appear as loosely aggregated groups of prismatic. They are present in mid-mesophyll and in the midvein phloem region. In *L. palustris* styloids or coarse raphides are found oriented vertically in the mesophyll.

Specimens examined:

L. alata Elliott, Arguelles 3, Mississippi. *L. arcuata* Walter, Hilsenbeck 668 (USF), Florida. *L. caparosa* (Cambess.) Hara, Ramamoorthy & Jones 118, Brazil. *L. decurrens* Walter, Raven 26469, Arkansas. *L. densiflora* (Micheli) Ramamoorthy, Ramamoorthy 650, Amazonas, Brazil. *L. erecta* (L.) Hara, Hatschbach s.n., 1976, Brazil. *L. lagunae* (Morong) Hara var. *paraguayensis* (Chodat) Munz, Ramamoorthy 1019, Paraguay, cult. MO. *L. leptocarpa* (Nutt.) Hara, Raven 26491, Arkansas. *L. linearis* Walter, Boufford & Wood 18899, North Carolina. *L. longifolia* (DC.) Hara, Ramamoorthy & Jones 115, Brazil. *L. maritima* Harper, Hilsenbeck 669 (USF), Florida. *L. microcarpa* Michaux, Boufford 18047, Florida; Hilsenbeck 667 (USF), Florida. *L. myrtifolia* (Cambess.) Hara, Ramamoorthy et al. 81, Brazil. *L. nervosa* (Poir.) Hara, Hatschbach s.n., 30 Jan 1976, Brazil. *L. palustris* (L.) Elliott, Boufford 18562, Florida; Willingham 598, Georgia; Arguelles 2, Mississippi. *L. peploides* (Humboldt, Bonpland & Kunth) Raven subsp. *glabrescens* (O. Kuntze) Raven, Raven 26493, Arkansas. *L. peruviana* L., Anderson 4082 (FSU), Florida. *L. pilosa* Walter, Boufford 18496, Florida. *L. polycarpa* Short & Peter, Raven 26523, Missouri. *L. sedoides* (Humboldt, Bonpland & Kunth) Hara, Croat 38286, Panama. *L. sericea* (Cambess.) Hara, Ramamoorthy et al. 68, Brazil. *L. spathulata* Torrey & Gray, Boufford 18564, Florida. *L. suffruticosa* Walter, Hilsenbeck 670 (USF), Florida. *L. virgata* Michaux, Willingham 597, Georgia.

Oenothera (Figs. 46, 47)—Specimens are about evenly divided among dorsiventral and isobilateral anatomy. Laminas are very thin (120 μ m) ranging to very

thick (490 μm). Epidermal layers are equally thick or much thicker adaxially. No cuticle is apparent except at the margins where, in some specimens, sharp ridges are formed. Stomata are equally common on both surfaces. Trichomes were not seen in a third of the specimens. When present, trichomes are smooth-walled, striate-ridged, papillate, tuberculate, or echinate. They may be thin-walled or heavy-walled and lignified. The mesophyll is either well- or poorly differentiated and has a palisade consisting of two layers except for one layer in *O. scabra*. Midrib shape is quite variable. In larger leaves the midrib has an abaxially prominent ridge. The ridge may be equally prominent adaxially as in *O. macrosceles* and *O. centauriifolia* or broadly grooved adaxially as in *O. grandiflora* and *O. grandis*. In smaller-leaved species, midribs are immersed as in *O. mendocinensis*, *O. scabra*, and *O. hookeri*. Midveins are broad arcs or narrow arcs. Phloem forms an abaxial band adjacent to the xylem. In leaves with large midribs and broad xylem arcs, single adaxial bands of phloem extend medially from the ends of the xylem and not immediately adjacent to the xylem adaxially. The midvein is generally surrounded by ground tissue extending to both epidermal surfaces except in the small midribs. The lateral boundary with the mesophyll is variable but predictable in the different shaped midribs. Margins may have a ridge of lignified and collenchymatous cells in *O. macrosceles*. Almost styloid-like coarse raphides occur in *O. macrosceles* and in a few other species. Most specimens contain fine raphides also or exclusively. They occur with or without gum sheaths, horizontal in mid-mesophyll, or vertically in the adaxial palisade. In some specimens heavy gum sheaths occur giving a sclereid-like appearance.

Specimens examined:

O. caespitosa Nutt. subsp. *macroglottis* (Rydb.) Wagner, Stockhouse & Klein, *Raven* 26536, Colorado. *O. centauriifolia* (Spach) Steudel, s. col., Uruguay, cult. MO. *O. elata* De Vries, *Stubbe s.n.*, 1969, California. *O. grandiflora* L'Hér. ex Ait., *Steiner* 1952, Mississippi. *O. grandis* (Britton) Smyth, *Benbow* 81, Texas. *O. macrocarpa* Nutt. subsp. *macrocarpa*, *Boufford & Lorence* 18868, Missouri. *O. macrosceles* A. Gray, *Gentry* 14568, Venezuela, cult. MO. *O. mendocinensis* Gillies ex Hooker & Arnott, *Santarius* 421, Argentina, cult. Düsselldorf. *O. parviflora* L., *Boufford* 18741, Ontario. *O. ravenii* Dietrich subsp. *argentinae* Dietrich, *Hecht* 31, Uruguay, cult. Düsselldorf. *O. rhombipetala* Nutt. ex Torrey & Gray, *Benbow* 82, Texas. *O. scabra* Krause, *Diers s.n.*, 1959, Argentina, cult. Düsselldorf. *O. spachiana* Torrey & Gray, *Straley* 751, Louisiana.

Stenosiphon (Figs. 44, 45)—The lamina is isobilateral and thick (310–380 μm). The epidermal layers are equally thick on both surfaces (20–25 μm) and covered with a smooth, well-developed cuticle. Trichomes were not seen. Stomata are common on both surfaces. The mesophyll is composed of well-formed columnar palisade cells, two layers beneath adaxial and abaxial epidermal layers. The midrib is large and protrudes as a rounded ridge symmetrically on either surface. The midvein is a broad arc with well-developed abaxial patches of phloem. Two adaxial bands of phloem adjacent to each edge of the xylem do not connect at the center. They are separated by ground tissue from the xylem. Midrib ground tissue surrounds the midvein. In the largest specimen, the chlorenchyma has a concave pattern at the midrib, is sharply demarcated from the ground tissue, and is symmetrically disposed laterally and dorsiventrally. In another specimen, the chlorenchyma is less sharply demarcated and has irregular vertical boundaries. The lamina has a well-defined ridge of thick-walled cells extending beyond the mesophyll. Tannins fill the cells in secondary vein sheaths, epidermal cells, and rows

of cells around the midvein. Coarse or fine raphides occur mostly in heavy red sheaths that are vertical in either palisade layer. Some fine raphides may occur horizontally without sheaths in mid-mesophyll.

Specimens examined:

S. linifolius (Nutt.) Heynh. *Raven* 26563, Kansas; *Benbow* 83, Texas.

Xylonagra (Figs. 27, 28)—The lamina of these dorsiventral leaves ranges from 130 to 170 μm in thickness. Epidermal layers are approximately equally thick and have no apparent cuticle. Stomata are common on both surfaces. Trichomes are uncommon and have boldly tuberculate walls. Mesophyll differentiation is poor with the single palisade layer occupying 40–50% of the mesophyll. The midrib forms a pronounced abaxial ridge and has a tendency toward a smaller adaxial ridge. The midvein varies from a broad arc to a very small arc. Phloem is mostly in an abaxial band with some adaxial phloem patches near the margins of the xylem arc. Midrib ground tissue surrounds the vein between epidermal layers. The mesophyll boundary is well marked and is convex laterally into the midrib ground tissue. Raphides are fine, mostly without gum sheaths, and are horizontal in the mid- or upper mesophyll.

Specimens examined:

X. arborea (Kellogg) Donn. Sm. & Rose, *D. Verity s.n.*, s. d., Baja California, Mexico, cult. LA and MO.

DISCUSSION

DISTRIBUTION OF ANATOMICAL FEATURES (see Table 1)

Leaves of Onagraceae are usually ovate, elliptical or linear with margins mostly entire or possessing small irregular teeth. They may be long- or short-petiolate and hydric to xeromorphic in structure. The leaves are exclusively dorsiventral in eight genera, exclusively isobilateral in only *Stenosiphon*, and with both conditions present in different species of seven genera. Five of the exclusively dorsiventral genera constitute entire tribes: *Circaea*, *Fuchsia*, *Hauya*, *Lopezia*, and *Ludwigia*. The other three, *Gongylocarpus*, *Heterogaura*, and *Xylonagra*, are placed in the Onagreae with seven other genera that have both dorsiventral and isobilateral leaves, as do the two genera of the remaining tribe, Epilobieae. It seems clear from this distribution that dorsiventral leaves are primitive in the family, and that isobilateral leaves have evolved on a number of occasions in the advanced tribes Onagreae and Epilobieae.

Midribs with the most prominent structure occur in leaves of the exclusively dorsiventral genera. As seen in transection, a marked abaxial protrusion may exceed an arc of 230° and contain a prominent semicircular midvein in species of *Ludwigia*, *Fuchsia*, *Lopezia*, and *Hauya*. This seems clearly to be the primitive condition for the family. In addition, a prominent adaxial ridge is common over the midrib in species of *Ludwigia*, *Fuchsia*, and *Gaura*. The majority of species of Onagraceae have midribs that are level with the mesophyll adaxially and that protrude abaxially in an arc varying from 90° to 180° . These midribs contain midveins that are either short or broad arcs. All isobilateral leaves have these

less curved midveins. The most highly developed isobilateral leaves have midribs that protrude adaxially and abaxially to the same degree. These include *Epilobium oreganum*, *Gaura angustifolia*, *G. demareei*, *G. parviflora*, *Oenothera centauriifolia*, *O. macrosceles*, and *Stenosiphon linifolius*.

Leaf margins between teeth are normally rounded in transection and contain no unusual histology. In a few strongly isobilateral species (*Calylophus berlandieri*, *Oenothera macrosceles*, *Stenosiphon linifolius*) the margin is comprised of a ridge of thickened cells. This zone, three to eight cells in from the margin, is collenchymatous or, in *O. macrosceles*, partially lignified. The margin zone is distinctly demarcated from the mesophyll and appears to provide strong mechanical protection.

Leaf teeth, apparently best formed in the genus *Fuchsia*, show an unusual hydathodal structure that Hickey (1981) has called the Fuchsioid tooth. It appears to have the same structure as the Rosoid tooth described by Hickey and Wolfe (1975). This structure has a subepidermal foramen or space that opens to the outside through one or more stomata. Beneath the foramen is a zone of elongated secretory cells that connect to a vein ending well within the margin (Figs. 48–51). The vein, appearing to be a single structure in transection, is seen in cleared leaves to be formed of a strong median vein flanked by two smaller veins that converge and fuse just beneath the area of secretory cells (Hickey, this symposium). The Fuchsioid tooth has been found among other families of Myrtales only in Lythraceae (L. Hickey, pers. comm.). It can be seen clearly in *Ludwigia*, *Lopezia*, *Fuchsia*, *Camissonia*, *Gaura*, and *Epilobium*, and is probably present in most other genera, even those with very reduced teeth. DeCastells et al. (1979) describe and illustrate this structure in five species of *Ludwigia*. Studies on the woody Saxifragaceae by Stern (1974, 1978) and Styer and Stern (1979a, 1979b) record the presence of a very similar type of hydathodal tooth.

The adaxial epidermal cells are up to twice as thick as the abaxial epidermal cells on dorsiventral leaves. The two layers are identical on many dorsiventral-leaved species and on all isobilateral leaves. Epidermal cells are most commonly horizontally elongate and convex on the outer surface but true papillate cells were recorded in *Lopezia miniata*. In other *Lopezia* species, epidermal cells are commonly of two sizes, conspicuously high and convex cells are interspersed with low flat cells. Midrib epidermal cells in *Hauya* are high and narrow in transection and elongate parallel to the midrib.

Little apparent difference in this study was noted between greenhouse-grown and field-grown plants regarding cuticle thickness. However this feature should be interpreted cautiously because Hull, Morton and Wharrie (1975) showed that cuticular development is normally much greater on outdoor grown plants. The cuticle layer is very thin in most specimens. It is generally thicker at the margins and above and below the midrib. The thicker marginal cuticle is usually longitudinally striate with striations being especially prominent in *Boisduvalia subulata*, *Calylophus berlandieri*, *Epilobium angustifolium*, *E. leptophyllum*, *E. oreganum*, *Gaura lindheimeri*, *G. parviflora*, *G. suffulta*, *G. villosa*, and *Oenothera macrosceles*. In *Hauya elegans*, the cuticle is flanged and conspicuously thickened in the grooves between epidermal cells.

Stomata are evenly dispersed over both epidermal layers in all genera except

TABLE 1. Leaf characters of Onagraceae.* (Continued on facing page.)

	Dorsiventral	Isobilateral	Midrib Protrudes Adaxially	Midrib Protrudes Abaxially	Midvein Semicircle	Midvein Broad Arc	Midvein Short Arc	Midvein with Adaxial Phloem	Abaxial Periphloic Fibers	Palisade Layers**	Mesophyll Well-differentiated	Mesophyll Poorly-differen.	Epidermal Thickness:	Adaxial = Abaxial	Adaxial > Abaxial
<i>Ludwigia</i>	+		+	+	+	+	a	+	a	1	+	a		+	a
<i>Hauya</i>	+			+	+			+	+	1	+				+
<i>Lopezia</i>	+		±	+	+	a	+	+		1(2)	+	+		+	+
<i>Fuchsia</i>	+			+	+	+	+	+	+	1	+	+		a	+
<i>Circaea</i>	+			+		+	+	+		1		+			+
<i>Epilobium</i>	+	+		+	a	+	+	+		1-2	+	+		+	a
<i>Boisduvalia</i>	+	+		+			+	+		1-2	±	+		+	
<i>Gongylocarpus</i>	+			+			+	+		1	+				+
<i>Gaura</i>	+	+	+	+		+	±	+		2-3	+	+		+	
<i>Camissonia</i>	+	+	a	+		+	a	+		1-3	±	+		+	±
<i>Gayophytum</i>		+				+		+		2		+			+
<i>Xylonagra</i>	+		±	+			+	+		1		+			+
<i>Calylophus</i>	+	+		+			+	+		1-3	+	a		+	
<i>Clarkia</i>	+	a		+			+	+		1-2	+	a		+	±
<i>Heterogaura</i>	+			+			+	+		1		+		+	
<i>Oenothera</i>	+	+	+	+		+	+	+		1-2	+	+		+	+
<i>Stenosiphon</i>		+	+	+		+		+		2	+			+	

* Symbols as follows: + = Character present, ± = Character weakly developed or tendency, a = present in a few species.
** Numbers in parenthesis are uncommon. In the case of isobilateral leaves, the number refers to the adaxial side only.

Fuchsia and *Hauya*, in which they are confined to the abaxial epidermis; and *Circaea* and *Lopezia*, in which both situations occur. In the Onagreae, stomata were lacking from the adaxial epidermis only in one sample of *Calylophus* and a few of *Clarkia*.

Trichomes are always simple, mostly unicellular, elongate and tapering to a point. They may be slightly expanded or constricted at the base. Bi-cellular trichomes were noted only in *Fuchsia lycioides*, *Ludwigia peruviana*, and *L. lagunae*. All trichomes in the family are usually thick-walled near the base and may or may not be lignified. Neighboring epidermal cells are not modified into buttresses. Trichome surfaces are smooth in many genera (at 400× magnification) but also occur with numerous types of surface features that do not seem readily to fall into a systematic pattern. The surface features are of the same magnitude

TABLE 1. Continued.

Stomata on Adaxial Epidermis	Stomata on Abaxial Epidermis	Styloids or Prismatic	Druses	Coarse Raphides	Fine Raphides	Horizontal, Mid-mesophyll	Random Position	Vertical in Palisade	Crystal Sheaths:	Absent	Thin	Thick	Elongate	Crystals Gum-replaced
+	+	a	+	+	+	+				+			+	+
	+	+	+		+	+						+		
a	+				+	+	+	+		+	+	+	+	+
	+			+	+	+	+	+			+	+		
a	+				+	+	+			+	+	+	+	
+	+			a	+	+	+	+		+	+	+	+	±
+	+			a	+	+	+					+		+
+	+	+		+	+	+						+		
+	+		a	a	+	+	+	+		+	+	+		
+	+			+	+	+	+	+				+	+	
+	+			+	+	+	+	+				+		
+	+				+	+				+	+	+		
+	+				+	+	+	a				+		
+	+			+	+	+		+		+	+	+	+	
+	+			+	+	+		+		+		+		

as pollen sculpturing and can be called rugulate, striate, or erose-rugulate with sculpturing patterns arranged in wavy vertical lines. Surface structural elements may be scabrate, gemmate, verrucate, or echinate in larger or more minute sizes (less than 1 μm) and uniformly dispersed. A thorough study of trichome surfaces in the Onagraceae using scanning electron microscopy would probably produce systematically valuable data.

The mesophyll in leaf transection may show a clear differentiation between a well-formed palisade and the adjacent spongy layer or there may be a gradual transition between the two epidermal layers. This distinction is noted in Table 1 as “mesophyll well- or mesophyll poorly differentiated.” There is generally a correlation between small midribs with small midveins and poor mesophyll differentiation. Palisade cells consistently constitute only one adaxial layer in *Cir-*

caea, *Fuchsia*, *Hauya*, *Heterogaura*, and *Ludwigia* but may be one or two layers in different species of other genera. Many studies on the ecological anatomy of tree species (e.g., Hanson, 1917; Drury, 1973) indicate that the degree of mesophyll differentiation is highly dependent on the degree of exposure to the sun. My experience with the Onagraceae suggests that, for several reasons, this is not an important factor. First, all of the herbaceous plants studied seem to grow normally in full sun with all leaves receiving a similar exposure. Secondly, multiple samples of a number of species have shown no significant structural differences in the mesophyll. Finally, those genera that would be most likely to show palisade layer differences due to shading in a forest environment (*Hauya*, *Fuchsia*) were uniform in my sample in having leaves with single palisade layers. Certainly the condition of having only one adaxial layer in the mesophyll must be primitive in the family, judged from the correlation with other features.

All petiolar traces and leaf midveins in the family have, abaxial to the xylem, a continuous band of primary phloem. In addition, all leaves with large conspicuous midveins have additional patches of phloem adaxial to the xylem. The term bicollateral as commonly described (Esau, 1965, p. 368) would seem to apply but is probably not appropriate. The adaxial phloem is not proximal to the protoxylem but is separated from it, often by a thick band of parenchyma. In those more primitive genera where deep semicircular traces are found (*Fuchsia*, *Ludwigia*, *Lopezia*, *Hauya*) the adaxial phloem may be scattered as random patches in the ground tissue within the semicircle. In genera with broad arcs (*Gaura*, *Oenothera*), the adaxial phloem is best developed lateral to the edges of the xylem and is generally not continuous across the trace. Secondary veins are usually collateral and surrounded by parenchymatous sheaths that differ little from spongy mesophyll in most species. Esau (1980, p. 181) has pointed out that almost no studies of dicotyledonous metaphloem patterns have been done, leaving the homologies of that tissue almost unknown.

Extraxylary fibers are found only in *Fuchsia*, *Hauya*, and *Ludwigia*. Both species of *Hauya* have a midvein surrounded by a layer of fibrous cells that are thick-walled but not birefringent. Fibrous tissue of the secondary veins extends transcurrently to both epidermal layers. Within *Fuchsia* only *F. arborescens* has been noted so far as having extraxylary fibers. *Ludwigia peruviana*, *L. polycarpa*, and *L. suffruticosa* have a sheath of fibers abaxial to the midvein phloem as well as sheaths surrounding the secondary veins. In Safranin-Fast Green preparations of the leaves of the three genera that show good differentiation and red-stained xylem, the extraxylary fibers stain a distinctive blue-green. In *Fuchsia* and *Ludwigia*, the fibers as well as the xylem are strongly birefringent.

Sclereids and laticifers are absent from the Onagraceae but calcium oxalate crystals are present in a diverse assortment of types. All genera contain packets of raphides but these vary markedly along systematic lines in orientation, in coarseness, and in covering. In *Ludwigia*, the raphides are surrounded by thin, non-staining membranes and are randomly or horizontally disposed in the mesophyll. In all other genera, the fine raphides are thinly or heavily sheathed in an amorphous material that has a strong affinity for Safranin-O. The raphide packets are horizontally or randomly (obliquely) oriented in the mesophyll or vertically oriented in the palisade layer. In the latter condition they are often the size and

shape of palisade cells in some species of *Fuchsia*, *Lopezia*, *Camissonia*, *Gayophytum*, *Gaura*, *Clarkia*, *Oenothera*, *Stenosiphon*, and *Epilobium*. In a few species of *Lopezia*, *Epilobium*, and *Boisduvalia*, the raphides may be totally replaced with the red-staining "gum," producing bodies having a strong superficial resemblance to sclereids. Coarse raphides occur in species of nine genera and often in the same tissues where the finer type is found. Prismatics or single rhombohedral crystals occur in a few species in the genera *Ludwigia*, *Gongylocarpus*, and *Hauya*. In *Ludwigia leptocarpa* the prismatics equal the leaf thickness in length and may be termed styloids. Druses are not common in the family but are abundant in a few species of *Ludwigia*, *Hauya*, and *Gaura*. The genus *Ludwigia* includes all forms of calcium oxalate crystals.

Angularly thickened collenchyma may be present or absent beneath epidermal layers in the midrib zone. Its presence is not particularly a function of leaf size or robustness nor was any systematic relationship discerned in this study.

TRENDS OF SPECIALIZATION

When interpreted carefully, leaf histology does have considerable systematic value as can be attested by such recent studies as Dickison (1975) on the Cunoniaceae, Drury (1973) on the Senecioneae-Compositae, or Dickison (1969) on the Dilleniaceae. The principal difficulty with leaf histology is that its trends of specialization are not yet well anchored in the fossil record. Recent stratigraphic studies of angiosperm pollen and leaf architecture (Doyle & Hickey, 1976) have demonstrated an increasingly regular and organized leaf architecture as one moves toward the present in the fossil record. In addition, Hickey and Wolfe (1975) showed that leaf architecture may become reduced in complexity within specific groups such as the Dilleniidae. For leaf histology, it will be necessary for the time being to rely on correlation of character states with other better known trends in well studied plant families such as the Onagraceae. In spite of Stebbins' (1974) caveat that correlations may be spurious if the character states being correlated are not functionally related, it should be possible, using the Onagraceae, to contribute to our knowledge of histological trends of specialization without making too many assumptions. As a result of much previous work we have documented morphoclines from wood, flowers, pollen, flavonoids, chromosomes, and breeding systems. Before discussing the trends in leaf histology, it is necessary to comment on the following inferences, which seem warranted based on this literature. These arguments are critical to any understanding of leaf specialization within the Onagraceae.

The family probably originated in South America in the late Cretaceous from ancestral stock related to other Myrtalean families (Raven & Axelrod, 1975; Raven, 1979). These families are presently distributed overwhelmingly in the southern hemisphere.

Within Onagraceae, *Ludwigia* clearly represents a distinct phylogenetic line, or one that is, in Hennigian terms, the "sister group" of all other Onagraceae (Eyde, 1981). Both it and *Fuchsia* have their greatest diversity and their most primitive species in South America at the present time, this relationship being consistent with the probable place of origin of the family, as just hypothesized.

Two other of the tribes that have been regarded as relatively generalized, those constituting the single genera *Hauya* and *Lopezia*, are restricted to Mexico and Central America, regions easily accessible to migration from South America at an early date (cf. Raven & Axelrod, 1975). *Circaea*, the only genus of the tribe Circaeae, was probably an early offshoot of one of these tribes. *Circaea* is restricted to the remnants of the Arcto-Tertiary Geoflora and best represented in temperate eastern Asia, with two species and a hybrid in North America and Europe. *Circaea* has a fossil record from Eurasia from the Oligocene onward (Eyde & Morgan, 1973).

The remaining tribes of the family, Onagreae, with ten genera, and Epilobieae, with two, appear to have originated in western North America in association with the development of the Madro-Tertiary Geoflora, perhaps in mid-Tertiary times (Raven, 1976; Raven & Axelrod, 1978).

The longest vessel elements (over 500 μm) are found in species of *Fuchsia*, *Ludwigia*, and *Hauya* (Carlquist, 1975). Most genera of the Onagreae and Epilobieae have vessel elements that are generally considerably shorter in both mean and range. The most extensively developed secondary xylem in the Onagraceae is found in *Fuchsia* and *Hauya*, with somewhat smaller woody stems found in a few species of *Ludwigia*, *Lopezia*, and *Epilobium*, very little wood in the Onagreae, and none in *Circaea*. Since none of these show any signs of having a secondarily derived wood anatomy (Carlquist, 1975), the xylem trends, along with biogeographic data, are possibly the best arguments for the vegetative primitiveness of *Fuchsia*, *Ludwigia*, *Lopezia*, and *Hauya*. In leaf architecture (Hickey, 1980, this symposium), *Fuchsia* appears to be the most generalized and has the best developed tooth and vein architecture. All other genera appear to constitute a reduction series. Interxylary phloem, certainly an advanced feature, is lacking in *Ludwigia*, *Fuchsia*, and *Hauya*, and present in the more advanced *Lopezia*, Onagreae, and Epilobieae (Carlquist, 1975). The latter two groups lack stipules, another advanced feature.

Summarizing this material briefly, *Ludwigia* represents a phylogenetic line separate from all other Onagraceae. Among the remainder of the family, *Fuchsia* and *Hauya* are the two least specialized genera, with *Circaea* and *Lopezia* related but clearly more specialized in certain respects, especially those concerned with floral morphology. The two most specialized groups, as judged by any criteria, are certainly the Epilobieae and Onagreae, tribes that might or might not share a common ancestor.

On the basis of the foregoing studies, one can best read the morphoclines in leaf histology of the Onagraceae as an overall reduction in histological complexity. Leaves have become smaller, less vascularized, and the vascularization has changed from a broad semicircle to a short arc. This is related to the less prominent abaxial midrib protrusion, which is probably less necessary for support in smaller leaves. In the three genera where extraxylary fibers occur, they are found in the species which have the largest midveins.

Among cellular inclusions, druse crystals and styloids are present in *Ludwigia* and *Hauya*. In addition, druses occur in *Gaura* and prismatics in *Gongylocarpus*, both of the Onagreae. The ability to make these crystals has apparently been lost in other evolutionary lines of the family. Of the various raphide forms, coarse

TABLE 2. Proposed leaf character state assignments for the Onagraceae*.

Character	Primitive State (0)			Advanced State (1)
Stipules	present			absent
Structure	dorsiventral			isobilateral
Midribs	prominent			reduced
Midveins	semicircle		broad arc (0.5)	short arc
Margins	rounded			thickened edge
Extraxylary fibers	present			absent
Stomata	abaxial only			adaxial also
Trichomes	bi- or multicellular			unicellular
Mesophyll	clearly differentiated			poorly differentiated
Palisade layer	single			double
Adaxial phloem	present			absent
Styloids/Prismatics	present			absent
Druses	present			absent
Raphide texture	coarse			fine
Raphide orientation	horizontal		random position (0.5)	vertical in palisade
Raphide sheaths	very thin (0)	thin (0.3)	thick or long (0.6)	replaced (1)

* Character states of 0 = primitive and 1 = advanced are used in Table 3 to score all genera for all characters listed here. Fractional numbers are values assigned to discernable intermediate states along a single morphocline.

raphides may, for several reasons, be proposed as a transition stage leading to fine raphides. The coarse raphides occur in randomly oriented cells in mid-mesophyll in leaves where fine raphides are also present. Whenever fine raphides are covered with thick and/or elongated sheaths, or are oriented vertically in the palisade layer, the coarse raphides are usually horizontally or randomly oriented in mid-mesophyll and without such other features. The thickening of fine raphide sheaths appears to be a step in a sequence leading to their final replacement by the sheath material. The isobilateral and/or reduced leaves are the type that most commonly have vertical thick-sheathed raphides or gum-replaced raphides in the palisade layers.

Table 2 includes a number of proposed trends of specialization that can be supported by the data. Character state figures are assigned ranging from 0 to 1 with "0" indicating the primitive state. In Table 3, leaves of the genera of Onagraceae are assigned values using the character states and values listed in Table 2. A range of 0 to 1 for a particular genus and character indicates that both character states are present in different species of the genus. Where a total range, such as 1–6 is given (e.g., *Ludwigia*), it is likely that only a few species, if any, would be unspecialized in all or most characters (i.e., have an index of advancement total of "1"). Another species may have all of the advanced states and therefore be classed as a "6." Most commonly, a given species may have various combinations of advanced and primitive states, a circumstance that should be further explored genus by genus. In this paper, the range totals for each genus are given in Table 3 as a means of comparing the genera and as a means of noting the evolutionary depth within the family. Note that larger genera show greater ranges of variation. It can be validly concluded that reduction in leaf structural complexity, the development of isobilateral leaves, and the specialization of crys-

TABLE 3. Leaf histology advancement index for genera of Onagraceae*.

	Stipules	Lamina Structure	Midrib	Midvein	Margin	Extraxylary Fibers	Stomata	Trichomes	Mesophyll Differentiation	Palisade	Adaxial Phloem	Styloids/Prismatics	Druses	Raphide Texture	Raphide Orientation	Raphide Sheaths	TOTAL
<i>Ludwigia</i>	0	0	0-1	0-1	0	0	1	0-1	0	0	0-1	0	0	0-1	0	0	1-6
<i>Fuchsia</i>	0	0	0-1	0-1	0	0	0	0-1	0-1	0	0-1	0	1	0-1	0-1	0-6	2-9.6
<i>Hauya</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0-5	.6	2.6-3.1
<i>Lopezia</i>	0	0	0-1	0-1	0	1	1	1	0-1	0-1	0-1	1	1	1	0-1	0-1	6-13
<i>Circaea</i>	0	0	1	1	0	1	1	1	1	0	0-1	1	1	1	0-5	0-6	9-11.1
<i>Gongylocarpus</i>	1	0	1	1	0	1	1	1	0	0	1	0	1	0-1	0	.3	8.3-9.3
<i>Epilobium</i>	1	0-1	1	1	0	1	1	1	0-1	0-1	0-1	1	1	0-1	0-1	0-6	8-14.6
<i>Boisduvalia</i>	1	0-1	1	1	0	1	1	1	0-1	0-1	0-1	1	1	0-1	0	0-1	8-14
<i>Oenothera</i>	1	0-1	1	1	0-1	1	1	1	0-1	0-1	0-1	1	1	0-1	0-1	0-6	8-15.6
<i>Gaura</i>	1	0-1	1	1	0	1	1	1	0-1	1	0-1	1	0	0-1	0-1	0-1	8-14
<i>Camissonia</i>	1	0-1	1	1	0	1	1	1	1	0-1	0-1	1	1	0-1	0-1	3-6	9.3-14.6
<i>Calylophus</i>	1	0-1	1	1	0-1	1	1	1	0-1	0-1	0-1	1	1	1	0-1	0-6	9-15.6
<i>Clarkia</i>	1	0-1	1	1	0	1	1	1	0-1	0-1	0-1	1	1	1	0-1	0-3	9-14.3
<i>Xylonagra</i>	1	0	1	1	0	1	1	1	1	0	0-1	1	1	1	0	0-3	10-11.3
<i>Heterogaura</i>	1	0	1	1	0	1	1	1	1	0	0	1	1	1	0-1	.3	10.3-11.3
<i>Stenosiphon</i>	1	1	1	1	1	1	1	1	0	1	0	1	1	0-1	0-1	0-6	11-13.6
<i>Gayophytum</i>	1	1	1	1	0	1	1	1	1	1	0	1	1	1	0-1	.6	12.6-13.6

* Character state codes are as listed in Table 2. Higher numbers indicate greater advancement. See text for further discussion.

tals, are changes that have taken place repeatedly in many genera. To postulate otherwise would imply that structural elaboration and reduction have proceeded back and forth, a conclusion that does not harmonize with data from any of the recent monographs that have been done on a number of the genera (e.g., Ramamoorthy, 1980, on *Ludwigia*; Wagner, in prep., on *Oenothera*; Raven & Gregory, 1972, on *Gaura*; Hoch, 1978, on *Epilobium*; Plitmann et al., 1973, on *Lopezia*). In each case, the leaves that would be classed here as unspecialized are placed in the more generalized sections based on comprehensive taxonomic criteria.

INTRAFAMILIAL RELATIONSHIPS

Eyde's (1977, 1981) studies of *Ludwigia* demonstrate that its floral anatomy is distinct from that of other Onagraceae, as mentioned above. Its central and transseptal ovular supplies, unusual nectary position, and ancient fossil record (Eyde & Morgan, 1973) suggest that the genus is a sister group to all other Onagraceae. Leaf anatomy supports this contention. The anatomy of *L. peruviana* (sect. *Myrtocarpus*) as well as that of a few species from sects. *Macrocarpon*, *Oligospermum*, *Humboldtia*, *Ludwigia*, and *Seminuda*, shows an elaborate midrib structure not approximated in any other genus. This is marked by the pronounced and flattened adaxial ridge of the midrib into which palisade mesophyll laterally intrudes. While at least one other genus may have one or another of *Ludwigia*'s features (e.g., druses occurring also in *Hauya* and *Gaura*), its anatomy among the more generalized sections with which it is commonly compared is absolutely distinguishable. In fact, its midrib structure has not been described from any other angiosperm. It should be noted that the species with less elaborate or reduced leaf structures in any genus of Onagraceae cannot generally be diagnosed or assigned to a genus with certainty.

Hauya has been considered to be the basal genus of the Onagreae (Raven, 1964) but is recently considered to belong in its own tribe, Hauyeae (Raven, 1979). Leaves of the genus bear no resemblance to any of the Onagreae, all of which are much more reduced (Table 3). Its arborescent habit, lack of adaxial stomata, and lack of a prominent adaxial midrib ridge separate it from *Ludwigia*. Separation from *Fuchsia* is not as easy. *Hauya*'s styloids and druses are not found in *Fuchsia* but the two genera are otherwise generally similar, especially in floral morphology and habit, and, with *Ludwigia*, are unique in Onagraceae in lacking interxylary phloem. Shoot apex studies (Keating, in prep.) indicate that *Hauya* has a leaf primordium configuration similar to that of *Fuchsia*, but differs in two important respects. Its young leaf primordia (in both species) show basal concrescence and the stipules emerge at a lower level. Otherwise, the shoot apices of the two genera closely resemble each other. The basic chromosome number in *Hauya* ($x = 10$), and possibly also the chromosome morphology as seen in mitosis (Kurabayashi et al., 1962), are derived as compared with that of *Fuchsia*, *Circaea*, and primitive species of *Lopezia* ($x = 11$).

It has been suggested (D. Boufford, pers. comm.) that *Fuchsia* may share an immediate common ancestor with the circumboreal *Circaea*, a genus that has structurally reduced leaves and could therefore have been derived from a *Fuch-*

sia-like ancestor. *Circaea* has had a fossil record since the Oligocene and its distinct flavonoid biochemistry suggests no clear relationships (Boufford, Raven & Averett, 1978). Its leaf structure suggests a *Fuchsia*-like plant that has lost a large midvein and all crystals but raphides. The relationship does not appear to be direct, and the similarity is probably based on shared ancestral (generalized) features that do not reflect an immediate common ancestor. In other words, the demonstrated similarities neither prove nor disprove a direct relationship between *Fuchsia* and *Circaea*. The mitotic chromosomes of primitive species of *Lopezia*, with a gametic chromosome number of $n = 11$, closely resemble those of *Fuchsia* and *Circaea* (Kurabayashi et al., 1962).

Lopezia shares with *Ludwigia*, *Fuchsia*, and *Hauya* the presence of stipules and a large midrib and midvein in the larger-leaved species, but it shows several marked advances, including the reduced stamen number (2), highly zygomorphic flowers, and presence of interxylary phloem. The extraxylary fibers are lacking as are all crystal types except fine raphides. In these respects it is similar to *Circaea* but virtually all additional features examined serve to separate the two. *Lopezia* has one or two palisade layers, interxylary phloem in the wood (Carlquist, 1975), and heavy gum sheaths around raphides in almost all species examined. Horizontal raphide sheaths may extend far beyond the crystals to a total length of 240 μm in *L. suffrutescens*, *L. grandiflora*, and *L. riesenbachia*. In some other species, the vertical gum sheaths in the palisade layer seem to contain no raphides at all but instead assume the appearance of dense, red-staining macrosclereids. With these features, *Lopezia* also seems to have had an isolated, separate evolutionary development within the family. Like *Circaea*, it shares many features with the postulated common ancestor of *Fuchsia* and *Hauya*.

The tribe Epilobieae, containing ca. 200 species of *Epilobium* plus *Boisduvalia*, is clearly a natural group on the basis of its morphology, its dotlike heteropycnotic chromosomes and its habit (in most species) of shedding pollen as tetrads (Raven, 1976). Leaf anatomy is generally quite reduced causing difficulty in discerning morphoclines let alone determining trends of specialization. Specimens of *Boisduvalia* and *Epilobium* are quite similar in their array of variation. *Epilobium suffruticosum* (sect. *Cordylophorum*) is alleged to be similar to the ancestral type (Raven, 1976) on the basis of its suffruticose habit, floral morphology, and chromosome number. This species has a distinctive isobilateral leaf, a striate cuticle, and a centric organization of palisade around a very small midvein, features that give the leaf a very xeromorphic appearance despite the species preference for permanently moist places. Raven (1976) and Raven and Raven (1976) have proposed that the extinct hypothetical ancestors of *Epilobium* were diploid xerophytes. If this is true, many of the dorsiventral-leaved species of other sections may possibly have been derived from ancestors with isobilateral leaves. Extremely divergent within *Epilobium* is sect. *Chamaenerion* (cf., Keating, Hoch & Raven, 1982). *Epilobium angustifolium* and *E. latifolium* show dorsiventral structure and large midribs (for the genus) with well developed adaxial phloem over broad midrib arcs. Such anatomy suggests that sect. *Chamaenerion* may be a sister group to the other five sections and may have developed from a primitively mesomorphic ancestor. Alternatively, *E. dodonaei* and *E. fleischeri* of sect. *Chamaenerion*, with their very reduced vasculature and isobilateral struc-

ture, may be primitive ones similar to *E. suffruticosum*. *E. angustifolium* and *E. latifolium*, however, show no signs of being secondarily woody according to Carlquist's (1962) criteria. The two sections of *Boisduvalia* are more similar to *Epilobium*, excluding sect. *Chamaenerion*, than that section is to any other member of the tribe. Peter Raven (pers. comm.) has suggested that the sections of *Boisduvalia* may have been (independently) derived from *Epilobium*, and perhaps should not be treated as generically distinct from it; whereas perhaps *Chamaenerion*, with its possibly primitive habit of shedding its pollen singly, may be the "sister group" of all other Epilobieae.

The Onagreae comprises a group of ten genera that are restricted as native plants to the New World and best represented in western North America (Raven, 1979). Most of the genera have at least one or more distinctive leaf structures but leaves from perhaps the majority of the more derived species could be placed in any of a half dozen genera. Group 1 Onagreae (Raven, 1979) consists of *Camissonia*, *Gayophytum*, *Gongylocarpus*, and *Xylonagra*. *Camissonia*, with 61 species, is the largest genus and its leaves contain midribs of various size and structure. Each of the four genera has one or more distinctive but not diagnostic features among its species. *Camissonia* has raphide gum sheaths up to 300 μm long as does *Gayophytum*. *Xylonagra* has boldly tuberculate trichomes, and *Gongylocarpus* has prismatic crystals.

Group 2 Onagreae consists of *Calylophus*, *Clarkia*, *Gaura*, and *Heterogaura*. Of these, *Gaura* alone is strikingly distinctive. The largest leaves tend to have a pronounced rounded midrib adaxially and abaxially. The broad arc midvein and its surrounding ground tissue is flanked by a concave mesophyll laterally lining the midrib zone. Best development is seen in *G. parviflora* (sect. *Schizocarya*), *G. lindheimeri*, and *G. longiflora* (both sect. *Gaura*). *Clarkia* and *Heterogaura*, clearly closely related on other grounds, are absolutely coincidental anatomically. Each has a very reduced midrib and midvein structure. *Clarkia concinna* has a very short, curved, striate, and papillate trichome type and raphides often occurring in paired bundles in ovate-outlined heavy sheaths. *Calylophus* has short rounded trichomes, and may have striate-ridged cuticle over leaf margins like *Gaura*. In contrast to *Gaura*, however, *C. berlandieri* has a mechanical zone at the margin (probably collenchyma) reminiscent of *Stenosiphon*. Its isobilateral mesophyll is centrally arranged around a small midrib as in *Epilobium suffruticosum*, however.

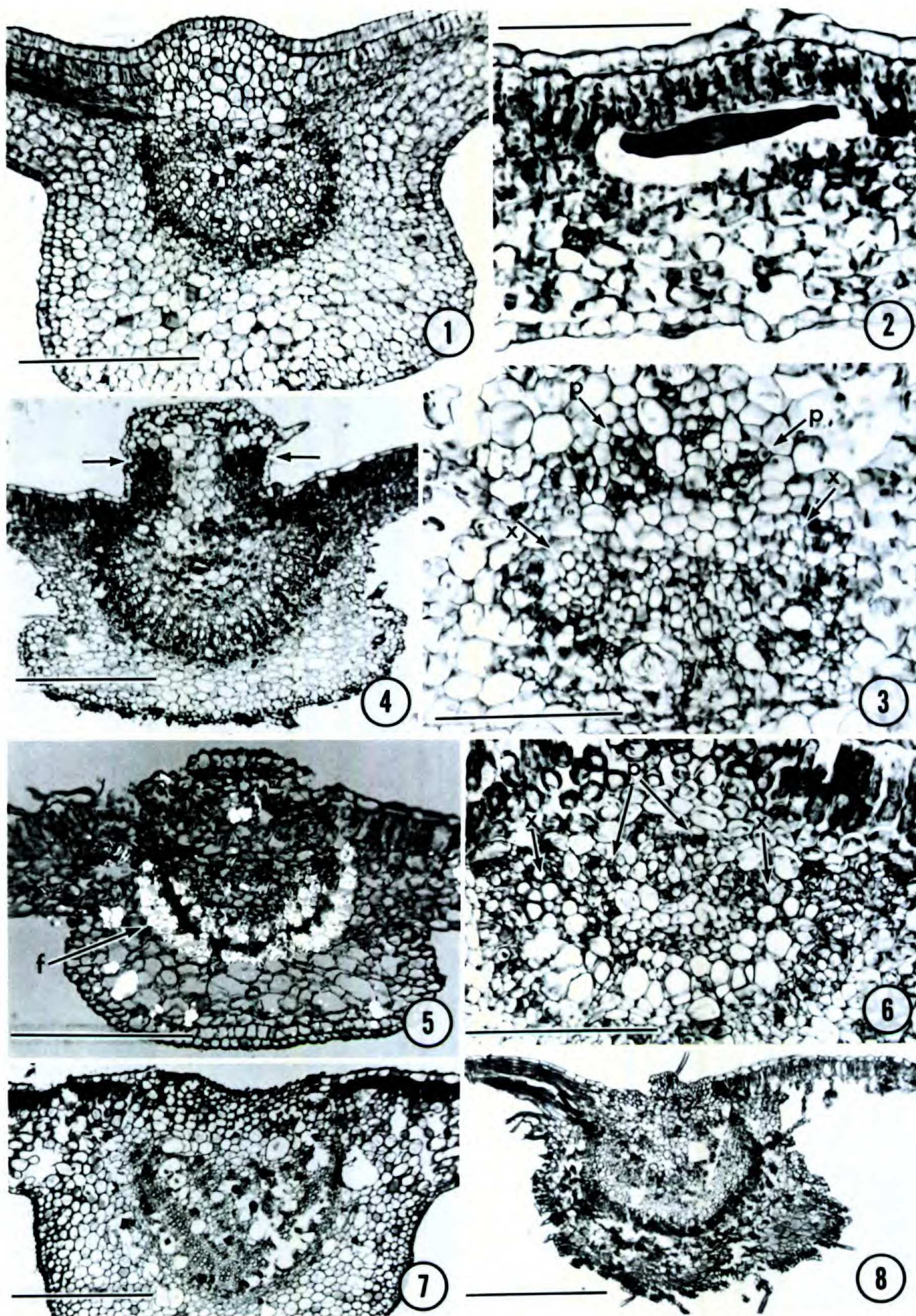
Group 3 Onagreae, with *Oenothera* and *Stenosiphon*, shows distinctive anatomy. Several patterns are found in *Oenothera* that range from the most massive leaf structure in the family (*O. macrosceles*, *O. grandiflora*) to thin and structurally reduced ones (*O. mendocinensis*). There is a tendency for the leaves with large midribs and broad arc midveins to be in the more primitive sections (Warren Wagner, pers. comm.), but my sample of this complex genus is insufficient to establish trends at present. *Stenosiphon linifolius* is quite easily distinguished from any *Oenothera* species with its isobilateral leaf containing pronounced and rounded midrib protrusions of equal height on both surfaces. The mesophyll within the midrib zone forms a lateral concave boundary against the midrib ground tissue. Its margin has a zone of thickened cells extending beyond the mesophyll a distance equal to the leaf thickness (310 μm). *Oenothera macrocarpa* (sect.

Megapterium) is the most similar (including midrib and margin anatomy) but *Stenosiphon* has a more strikingly symmetrical midrib. Also quite similar are the above mentioned *Gaura* species but the genera can be distinguished. The adaxial phloem band in *Stenosiphon* is separated from the xylem by the midrib ground tissue while in *Gaura* the adaxial phloem is quite close, perhaps truly bicollateral on the midvein. In addition, the margins of *Gaura* leaves have a sharply striate cuticle over an epidermis that is directly adjacent to mesophyll tissue. *Stenosiphon* margins have a smooth surface over a zone of marginal mechanical tissue. I believe, therefore, that the other structural similarities have a parallel origin.

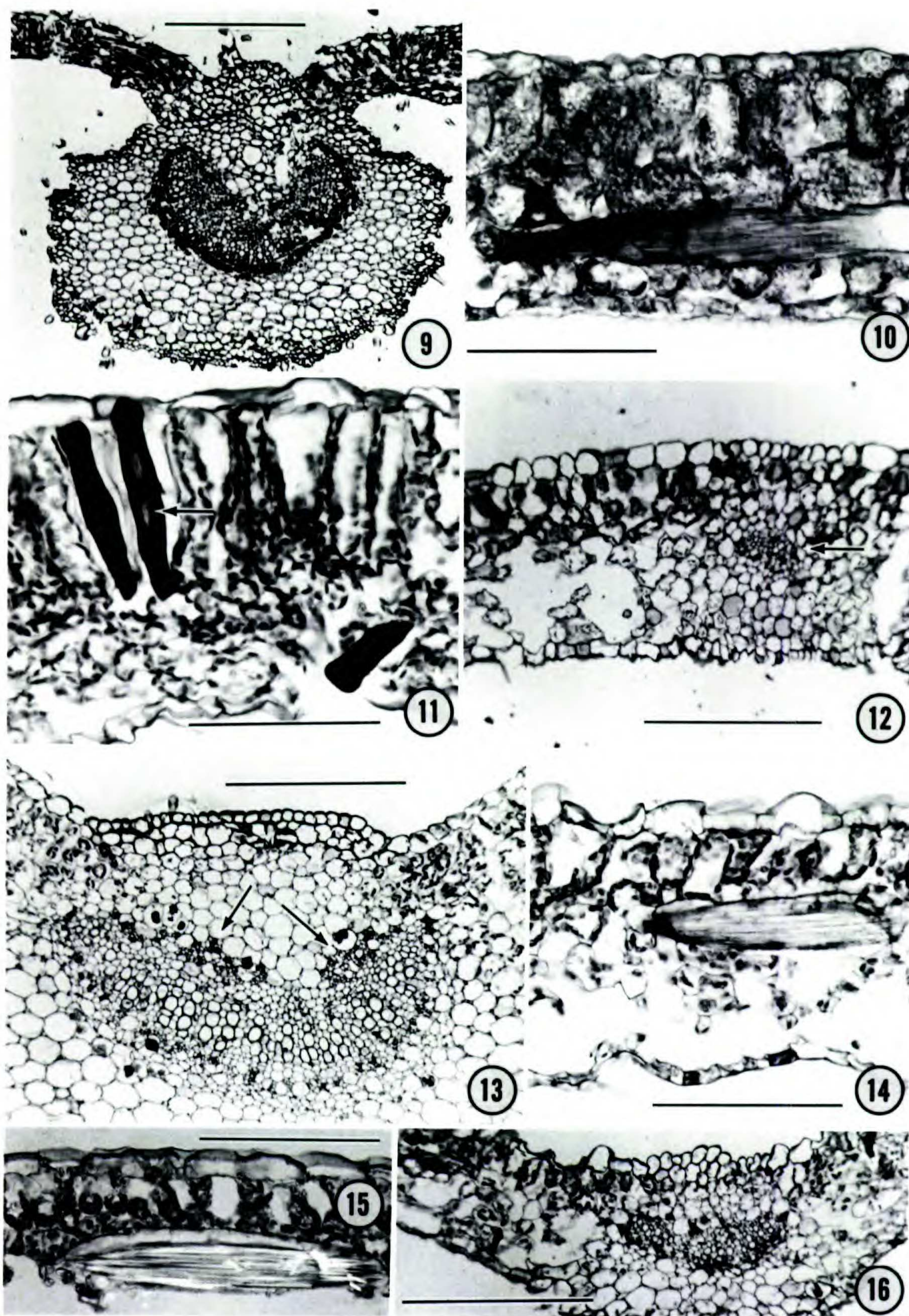
The principal question regarding the Onagreae remains whether evolutionary lines can be detected or whether the ten genera represent mostly isolated end lines of similar levels of advancement. With the data available, the question must remain open. A distinct and limited array of character states occurs in the Onagreae but not in any clear pattern. The character state analysis attempted here using punched cards and correlation matrices produced no discrete clusters, the character states showing instead almost a reticulate pattern among the genera. These leaves appear structurally simplified and efficient, carrying little in the way of remnants of a structurally more elaborate ancestry. The hypothesis of a common origin remains viable but so many of the genera have shown similar reduction sequences that much more refined data and analysis will be needed before the lines will be sorted out.

INTERFAMILIAL RELATIONSHIPS

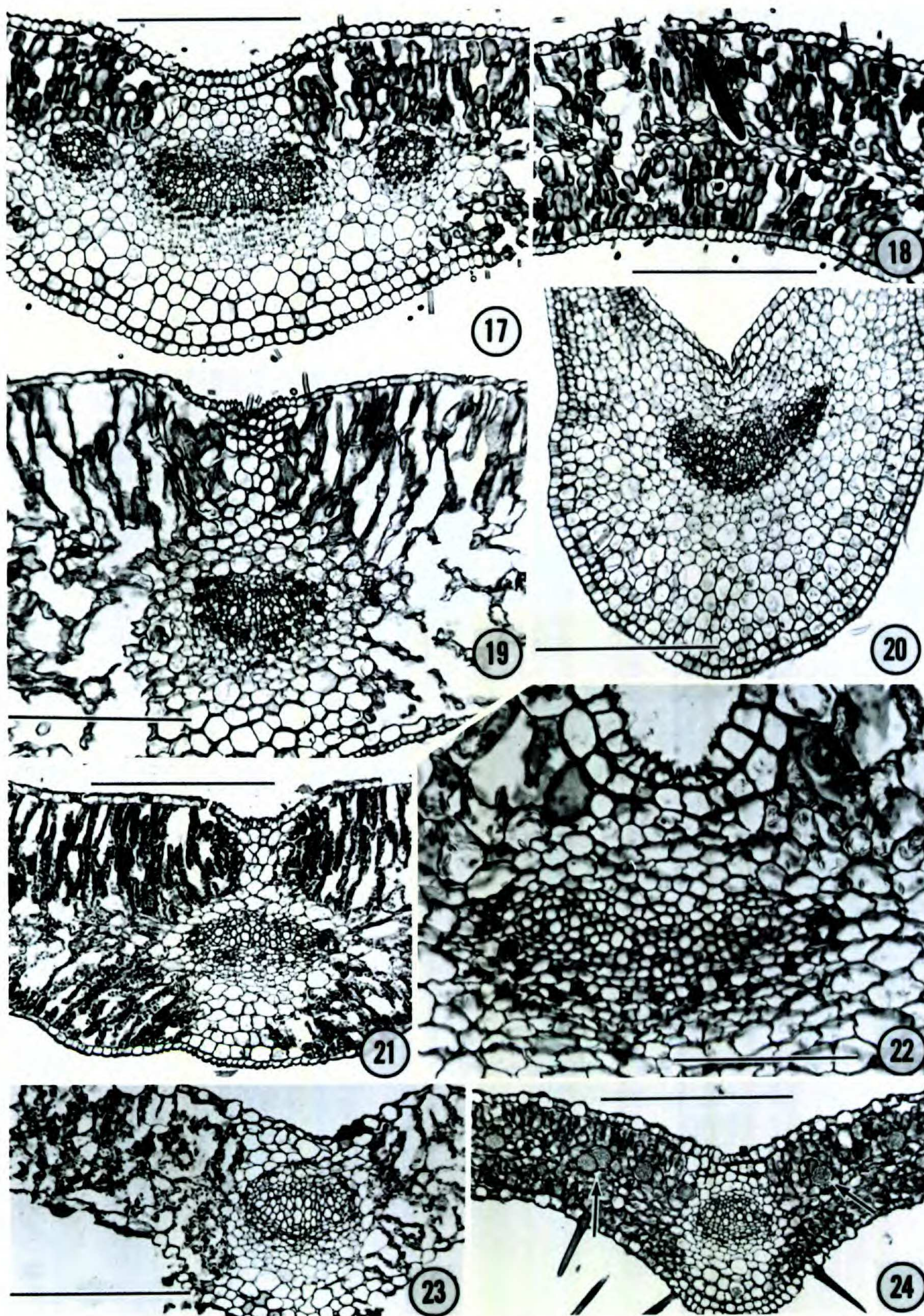
Carlquist (1975) stated that “. . . [wood] anatomical features prove unusually decisive in establishing relationships of the Onagraceae.” He stated that affinities seem greatest with the Lythraceae, Punicaceae, Sonneratiaceae, Crypteroniaceae, Combretaceae, and less strongly, with Melastomataceae. Unfortunately, with the present data available on other Myrtalean families, leaf anatomy proves unusually indecisive at the moment. The leaf structure of the other families of Myrtales, including their petiole anatomy, is generally much more complex than that of the Onagraceae. This would appear to provide corroboration for the idea that the Onagraceae represent a reduction series in these respects. Perhaps the most intriguing piece of data is the anatomy of the hydathodal tooth of the Onagraceae, which is also present in Lythraceae. The striking similarity of these teeth to the same feature found in several genera of woody Saxifragaceae by Stern (1974, 1978) and Styer and Stern (1979a, 1979b) may imply an ancestry directly out of the ancestral Saxifragales (of Takhtajan, 1969) for the Onagraceae, Lythraceae, and thus Myrtales in general. Until studies of Myrtalean leaf structure, now underway, are completed, further speculation will provide no useful insights.



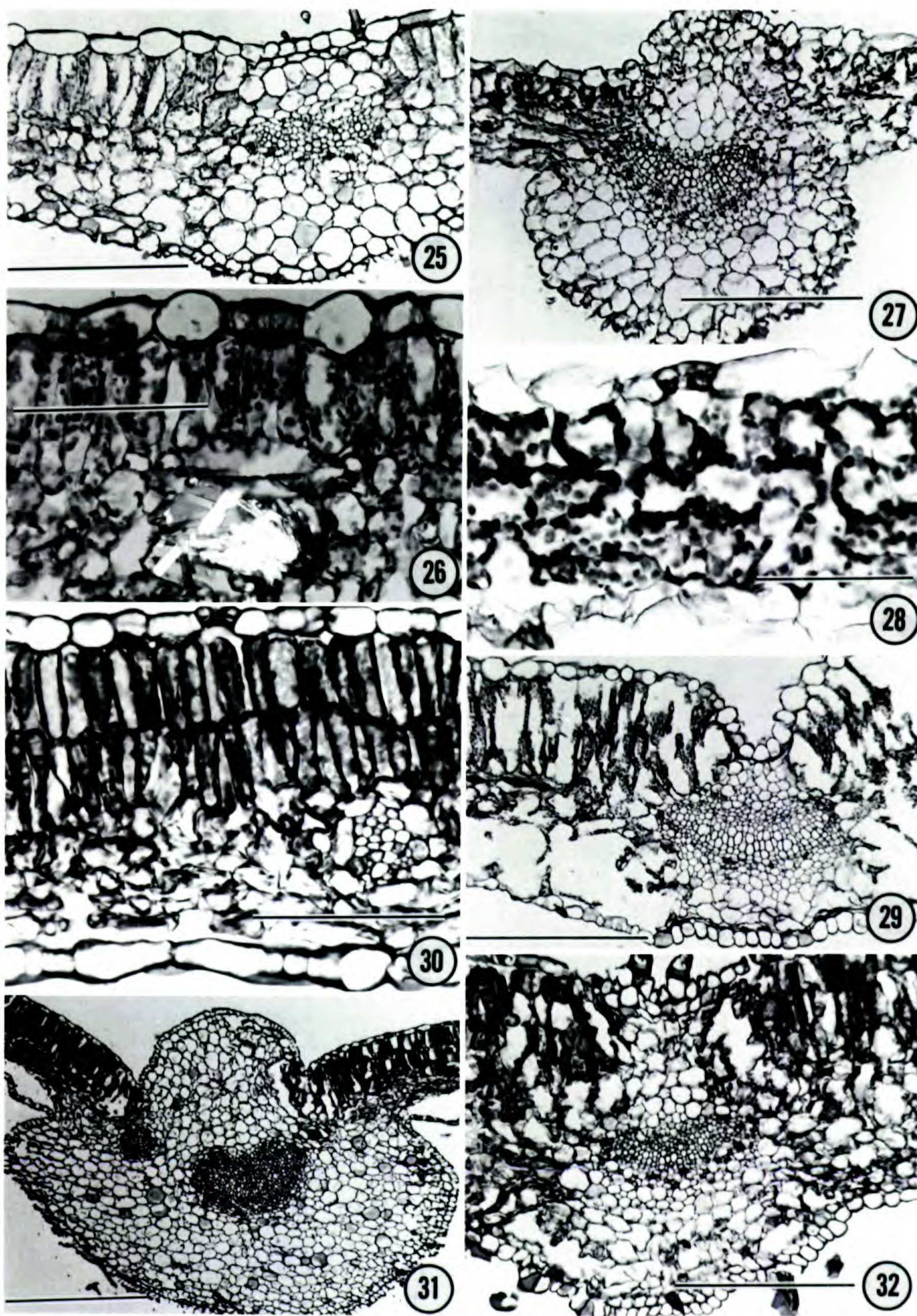
FIGURES 1-8. Leaf cross sections of Fuchsiaeae, Jussiaeeae, and Haueyeae.—1. *Fuchsia arborescens*, young leaf midrib. The vascular trace is semicircular.—2. *F. boliviana*, lamina section with raphide cell. Raphides are surrounded by a heavy elongated gum sheath.—3. *F. ravenii*, section of broad arc midvein showing adaxial phloem zone (p-arrows) well above the ends of the xylem (x-arrows).—4. *Ludwigia peruviana*, midrib section with semicircular vascular trace and mesophyll tissue in the adaxial ridge (arrows).—5. *L. suffruticosa*, midrib section under polarized light. Note light xylem semicircle surrounded by the dark band of abaxial phloem. Extraxylary fibers (f-arrow) surround the phloem.—6. *L. peploides*, midvein section with xylem semicircle (x-arrows) and adaxial phloem patches (p-arrows).—7. *Hauya heydeana*, midrib section showing semicircular vascular trace.—8. *H. elegans*, midrib section showing large semicircular vascular trace. Scale lines equal 500 μm for Figs. 4, 7, 8; 250 μm for Figs. 1, 5; 100 μm for Figs. 2, 3, 6.



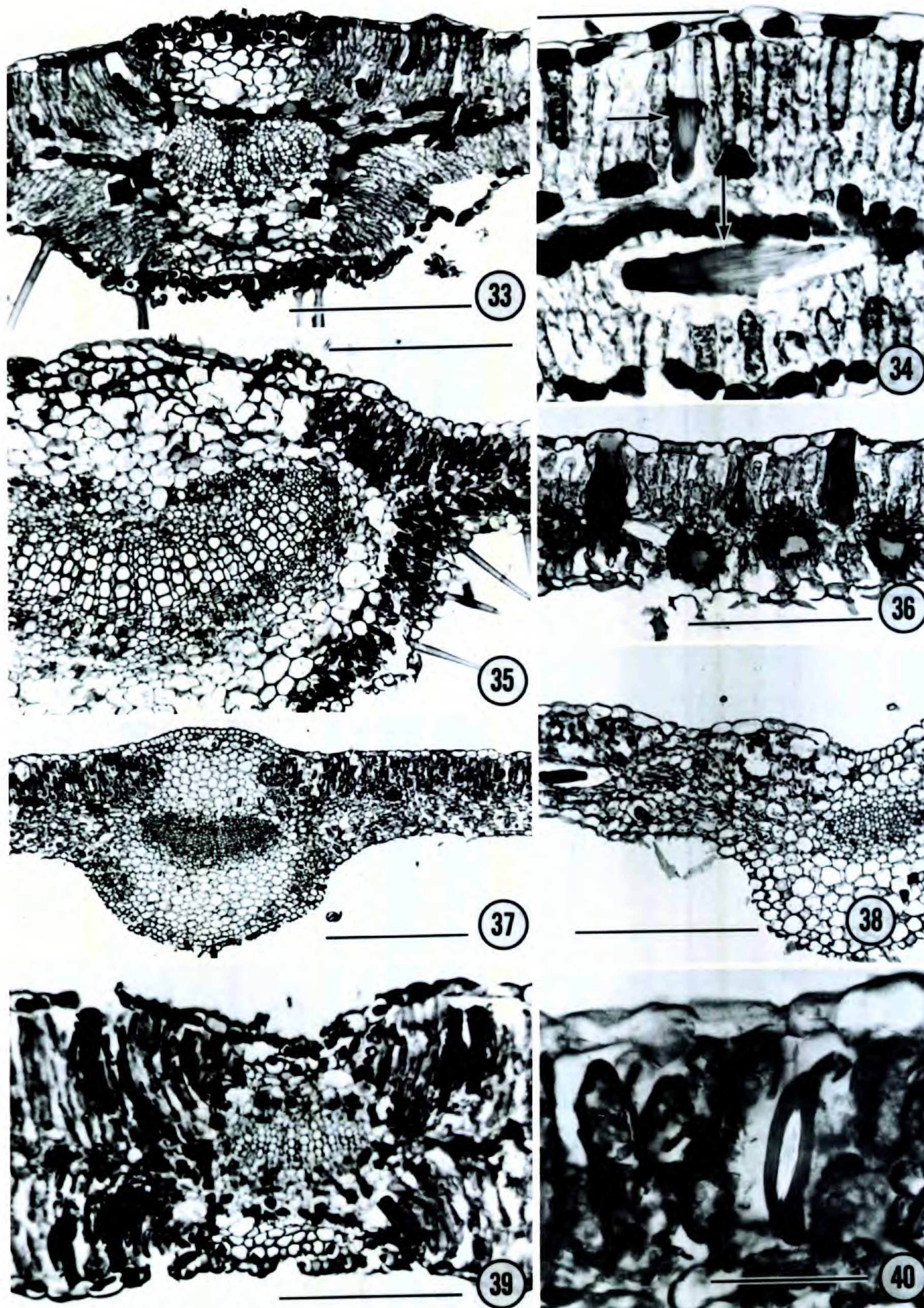
FIGURES 9-16. Leaf cross sections of Lopezieae and Circaeae.—9. *L. semeiandra*, midrib section. Note semicircular vascular trace and overall rounded appearance of the midrib outline.—10. *L. riesenbachia*, lamina with thick, elongated raphide sheath covering fine raphides.—11. *L. racemosa*, lamina with two thick raphide sheaths in the palisade. Raphides are barely visible (arrow).—12. *Circaea cordata*, short arc midvein immersed in a midrib that shows no adaxial or abaxial distention. Note short arc midvein (arrow).—13. *C. lutetiana*, midrib and midvein. Note the adaxial phloem (arrows) formed close to the protoxylem.—14. *C. erubescens*, lamina showing fine raphides horizontal in mid-mesophyll. Note the thin sheath.—15. *C. lutetiana*, adaxial half of lamina with unsheathed fine raphide bundle under polarized light.—16. *C. erubescens*, small midrib with broad arc midvein. Midvein-mesophyll boundary is poorly differentiated and no adaxial phloem is present. Scale lines equal 500 μm for Fig. 9; 250 μm for Figs. 12, 13, 15; 100 μm for Figs. 10, 11, 14, 16.



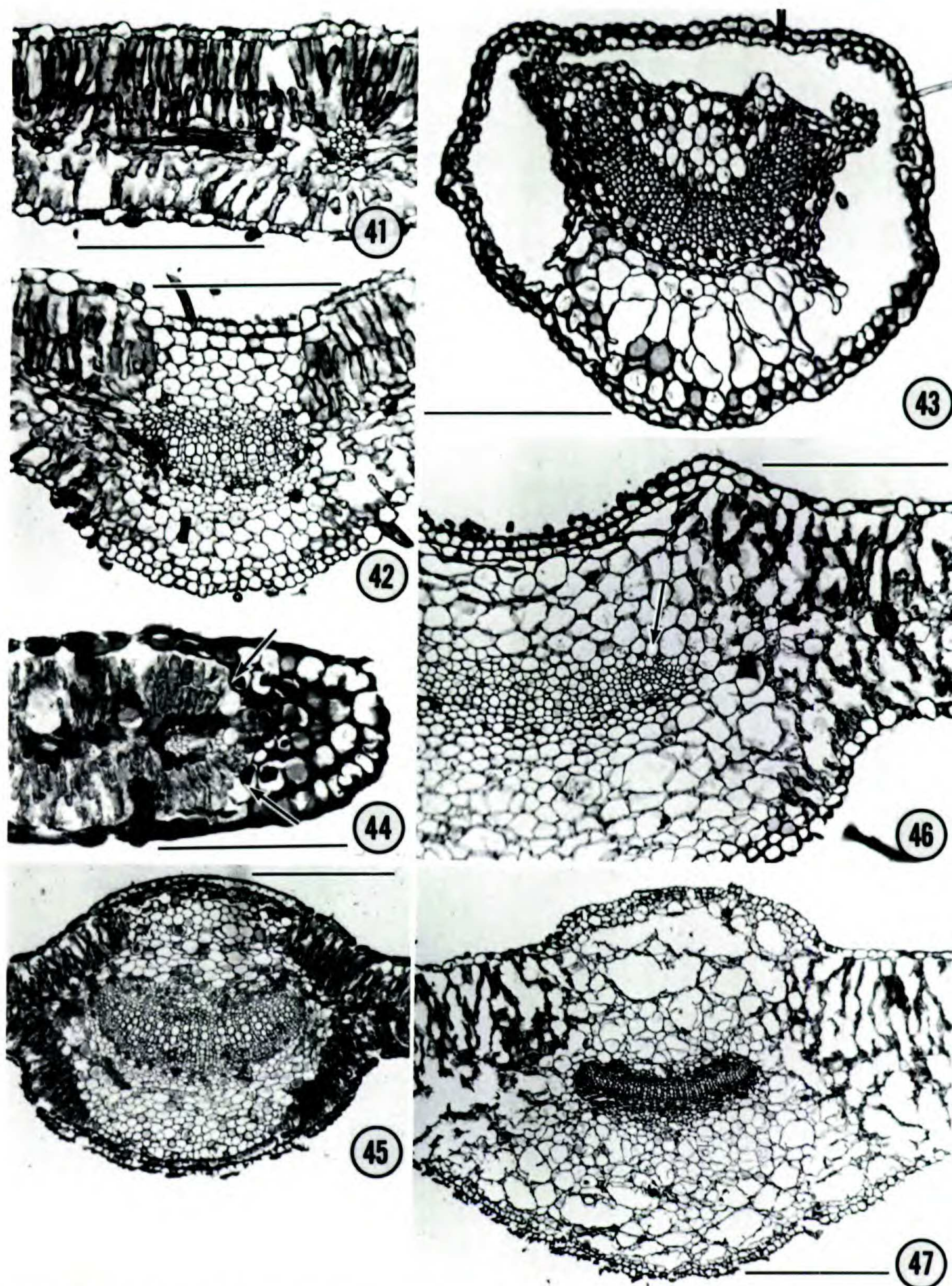
FIGURES 17-24. Leaf cross sections of Epilobieae.—17. *Epilobium suffruticosum*, midrib with broad arc midvein.—18. *E. suffruticosum*, isobilateral lamina with three palisade layers on both sides. Note the elongated vertical, thick-sheathed raphide cell.—19. *E. latifolium*, midrib with small arc midvein. Note the restricted zone of midrib ground tissue.—20. *E. pyrricolophum*, large midrib with large ground tissue area.—21. *E. dodonaei*, midrib of isobilateral leaf. Note small arc midvein surrounded by restricted ground tissue zone.—22. *E. glabellum*, broad arc midvein with no adaxial phloem.—23. *Boisduvalia macrantha*, midrib with small arc midvein.—24. *B. subulata*, midrib with small arc midvein. Raphide crystal cells (unsheathed) occur in cross section in a band in mid-mesophyll (arrows). Scale lines equal 250 μ m for Figs. 17-23; 100 μ m for Fig. 24.



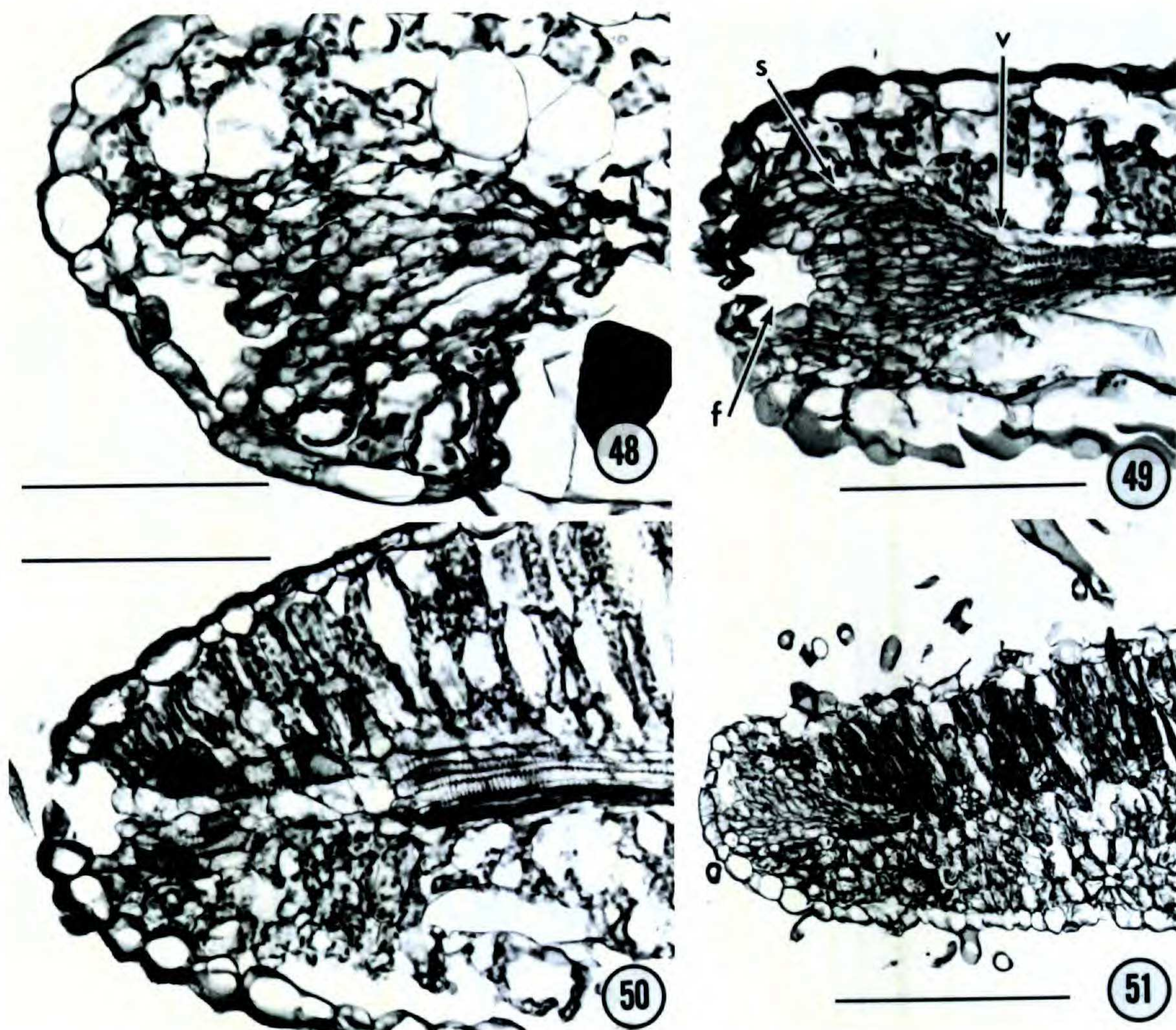
FIGURES 25–32. Leaf cross sections of group 1 Onagraceae.—25. *Gongylocarpus rubricaulis*, midrib with short arc midvein. Note poorly defined boundaries between the mesophyll and midrib ground tissue.—26. *G. rubricaulis*, lamina under polarized light showing coarse raphides.—27. *Xylonagra arborea*, midrib with abaxial and adaxial ridges.—28. *X. arborea*, lamina with adaxial stomate and a poorly differentiated mesophyll.—29. *Gayophytum heterozygum* midrib with a broad arc midvein under an adaxial groove. Midvein ground tissue does not surround the vein laterally.—30. *Camissonia ovata*, lamina with adaxial stomate and a well-differentiated lamina with two palisade layers.—31. *C. ovata*, large midrib with short arc midvein. Ground tissue zone is extensive.—32. *C. cheiranthifolia*, small midrib with a restricted midvein zone. Scale lines equal 500 μm for Fig. 31; 250 μm for Figs. 25, 27, 29, 32; 100 μm for Figs. 26, 30; 50 μm for Fig. 28.



FIGURES 33–40. Leaf cross sections of group 2 Onagreae.—33. *Gaura villosa*, midrib of isobilateral leaf. The short arc midvein has ground tissue restricted to patches above and below the midvein. Note centric orientation of palisade mesophyll near the midvein.—34. *G. villosa*, lamina with stored gummy or tanniniferous materials at the epidermal layers and in mid-mesophyll. Note fine raphides in gum sheaths, horizontal at mid-mesophyll and in the palisade layer (arrows).—35. *G. parviflora*, large midrib with broad arc midvein. Note mesophyll in the midrib zone forming a concave boundary with the midrib ground tissue.—36. *G. suffulta* subsp. *suffulta*, lamina with raphides in gum sheaths oriented vertically in the palisade layer and horizontally (in cross section) in the spongy mesophyll.—37. *G. lindheimeri*, midrib with anatomy similar to Fig. 35 above but with less strongly developed mesophyll in the midrib zone.—38. *Calylophus hartwegii*, midrib and lamina. Note poorly differentiated mesophyll and indistinct boundary with the midrib ground tissue.—39. *C. berlandieri*, midrib in isobilateral leaf with no surface distentions. Note centric arrangement of palisade cells near the midvein.—40. *C. berlandieri*, adaxial portion of lamina under polarized light showing raphide crystals in a thick gum sheath. Scale lines equal 500 μm for Fig. 37; 250 μm for Figs. 33, 35, 36, 38, 39; 100 μm for Fig. 34; 50 μm for Fig. 40.



FIGURES 41–47. Leaf cross sections of groups 2 & 3 Onagreae.—41. *Clarkia rubicunda*, lamina and secondary vein. Leaf is isobilateral with well-differentiated palisade cells.—42. *C. rubicunda*, midrib and midvein with well-differentiated mesophyll and midvein-mesophyll boundary.—43. *Heterogaura heterandra*, petiole showing semicircular vein. Large spaces in the ground tissue were filled with mucilaginous material.—44. *Stenosiphon linifolius*, isobilateral lamina with mesophyll ending (arrows) well within the mechanically strengthened margin.—45. *S. linifolius*, midrib with broad midvein arc. Note the palisade mesophyll intrusion into the midrib making a concave boundary with the midrib ground tissue.—46. *Oenothera grandis*, midrib with broad midvein and limited adaxial phloem (arrow). Note pronounced adaxial midrib groove bounded by a ridge.—47. *O. macrosceles*, large midrib with broad arc midvein. Scale lines equal 500 μm for Figs. 45, 47; 250 μm for Figs. 41–44, 46.



FIGURES 48–51. Leaf cross sections showing marginal hydathodal tooth glands.—48. *Lopezia nuevo-leonis*.—49. *Epilobium melanocaulon*.—50. *Camissonia claviformis*.—51. *C. cheiranthifolia*. In all figs., note stomatal opening to the subepidermal foramen (f-arrow). Vein ending (v-arrow) expands into secretory tissue (s-arrow). Scale lines equal 250 μ m for Fig. 51; 100 μ m for Figs. 48–50.

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